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THE EVOLUTION OF COLOR VISION IN INSECTS

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■ **Abstract** We review the physiological, molecular, and neural mechanisms of insect color vision. Phylogenetic and molecular analyses reveal that the basic *bauplan*, UV-blue-green-trichromacy, appears to date back to the Devonian ancestor of all pterygote insects. There are variations on this theme, however. These concern the number of color receptor types, their differential expression across the retina, and their fine tuning along the wavelength scale. In a few cases (but not in many others), these differences can be linked to visual ecology. Other insects have virtually identical sets of color receptors despite strong differences in lifestyle. Instead of the adaptionism that has dominated visual ecology in the past, we propose that chance evolutionary processes, history, and constraints should be considered. In addition to phylogenetic analyses designed to explore these factors, we suggest quantifying variance between individuals and populations and using fitness measurements to test the adaptive value of traits identified in insect color vision systems.

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INTRODUCTION

Studying the evolutionary ecology of insect color vision should be rewarding for two main reasons. The first is realization of the enormous diversity of visual conditions in which insects operate—for example, some fly at night, and others live in muddy freshwater—and of the habitats they have colonized, from glaciers and deserts to dense tropical forests to caves. Insects of a single genus, *Bombus* (the bumble bees), are found anywhere from Greenland to the Amazon Basin and from sea level to altitudes of $\leq$5800 m in the Himalayas (163). These habitats have not only differences in light intensity of several log units but also differences in the spectral composition of ambient light and in the color signals relevant for each species (34, 56, 100).

The second reason that studying the evolutionary ecology of insect color vision should be rewarding is that color receptors across species seem highly diverse, so they offer great potential for evolutionary adaptation. The number of different spectral receptor types found in one insect species can be as high as six, as in some flies (69) and as low as one if only particular eye regions are considered, as in the frontal eye of the owlfly *Ascalaphus macaronius* (63). The spectral range covered by these photoreceptors differs widely between species. The wavelength range to which the frontal eye of *A. macaronius* is sensitive is comparatively narrow [from 300 to 480 (63)], whereas the four, five, or even six different spectral receptor types present in some species of butterflies, dragonflies, and Hymenoptera (4, 20, 76, 104, 124, 126, 166) cover visual ranges that rank among the broadest ever described in animals (from $<$300 to $>$700 nm). In a single insect species, different parts of the eyes are often equipped with receptors of different spectral sensitivity (144), and sexual dimorphisms are not uncommon (16). Moreover, the shape of the spectral sensitivity functions and their maximum sensitivity values can differ between species (45, 69, 126).

Despite all of the variability, there appear to be conservative patterns in wavelength positioning of arthropod photoreceptors. It is surprising that animals occupying entirely different ecological niches, such as the beach isopod *Ligia exotica* (70), the nocturnal hawk moth *Manduca sexta* (161), the freshwater bug *Notonecta glauca* (24), and flower-visiting Hymenoptera (34), possess very similar sets of UV, blue, and green receptors, as do the larval ocelli of some Lepidoptera (80). The evolution of insect color vision cannot be understood without understanding the history of the insects. Our review thus considers adaptation primarily in the context of phylogeny and molecular biology. Other approaches to the study of evolutionary adaptation, such as population studies and biogeography, selection experiments, and fitness tests, are in their infancy (36).

VISUAL PIGMENTS AND THEIR SPECTRAL SENSITIVITY

A visual pigment is composed of a light-sensitive retinal-based chromophore and an opsin protein. Opsins are members of the G-protein-coupled receptor family and contain seven transmembrane (TM) domains. The helical TM domains

of an opsin form a binding pocket within which the chromophore sits. In this environment, specific amino acid side groups interact to shift the sensitivity of the short-wavelength (377- to 400 nm)-absorbing chromophore (141) to longer wavelengths of light. Both the amino acid sequence of the opsin protein and the chromophore affect the maximum absorption (λ_{max}) of the visual pigment. In the absence of filtering effects of other photoreceptor cells and screening pigments (reviewed below), the λ_{max} value of the visual pigment should approximately match the peak sensitivity of the photoreceptor cell expressing that pigment.

Long-wavelength visual pigment absorption spectra are composed of two peaks, a larger α peak and a smaller β peak near the UV wavelength, caused by the *cis* band of the chromophore. As the visual pigment peak wavelength (λ_{max}) value is blue shifted, the β peak gradually disappears under the larger α peak. Equations have been derived that describe the transformation of these curves, and given the λ_{max} value of a visual pigment alone, these equations can be used to generate the absorption spectrum curve (145). Different chromophores have different templates, and the existence of such templates allows the calculation of spectra from partial data and the possibility of testing whether a particular kind of chromophore is being used by the animal under study (e.g. 98).

Most insects use only one, or at most, two chromophores, either 11-*cis* retinal (A1) or the (3R) and (3S)-enantiomers of 11-*cis* 3-hydroxyretinal (A3) (141). The λ_{max} value of all-*trans* A1 without an opsin (383 nm) is similar to the λ_{max} of all-*trans* A3 (379 nm) (141). Reconstituted with bovine opsin, however, the difference in λ_{max} between reconstituted A1 and A3 varies from 6 to 12 nm, depending on the experimental conditions (60). With one or two chromophores in a single individual, paired with different combinations of opsins, insects generate up to six spectral classes of photoreceptors and several classes of ommatidia that are composed of different subsets of these spectrally-distinct photoreceptor cells (85).

The earliest chromophore in insects appears to have been A1, with some insects acquiring the ability to use A3 near the end of the Cretaceous period (141). Nine insect orders (Plecoptera, Hemiptera, Neuroptera, Coleoptera, Hymenoptera, Mecoptera, Diptera, Trichoptera, and Lepidoptera) contain a majority of the species that use either A1 or A3, as well a few species that use both (see Figure 1). All other insect orders use only A1 (62, 141). Because A1 and A3 differ slightly in λ_{max} when reconstituted with the same opsin, it is possible to achieve spectral tuning by varying the chromophore. Indeed, this may be a strategy that is widely used by the order Odonata, in which 44 of 46 species use both A1 and A3 as chromophores. The relatively small amount of variability of chromophores within other insect orders, however, indicates that this is unlikely to be the primary strategy (141).

Why do insects vary their chromophores at all? Seki & Vogt (141) consider the answer to lie in the biosynthetic precursors of A1 and A3, which are carotene and xanthophylls obtained from plants. Xanthophylls (precursors to A3) are derived from carotene (precursor to A1) in a process that requires molecular oxygen. The large increase in atmospheric oxygen during the Carboniferous period may have increased the reaction rate of xanthophyll synthesis and hence increased the

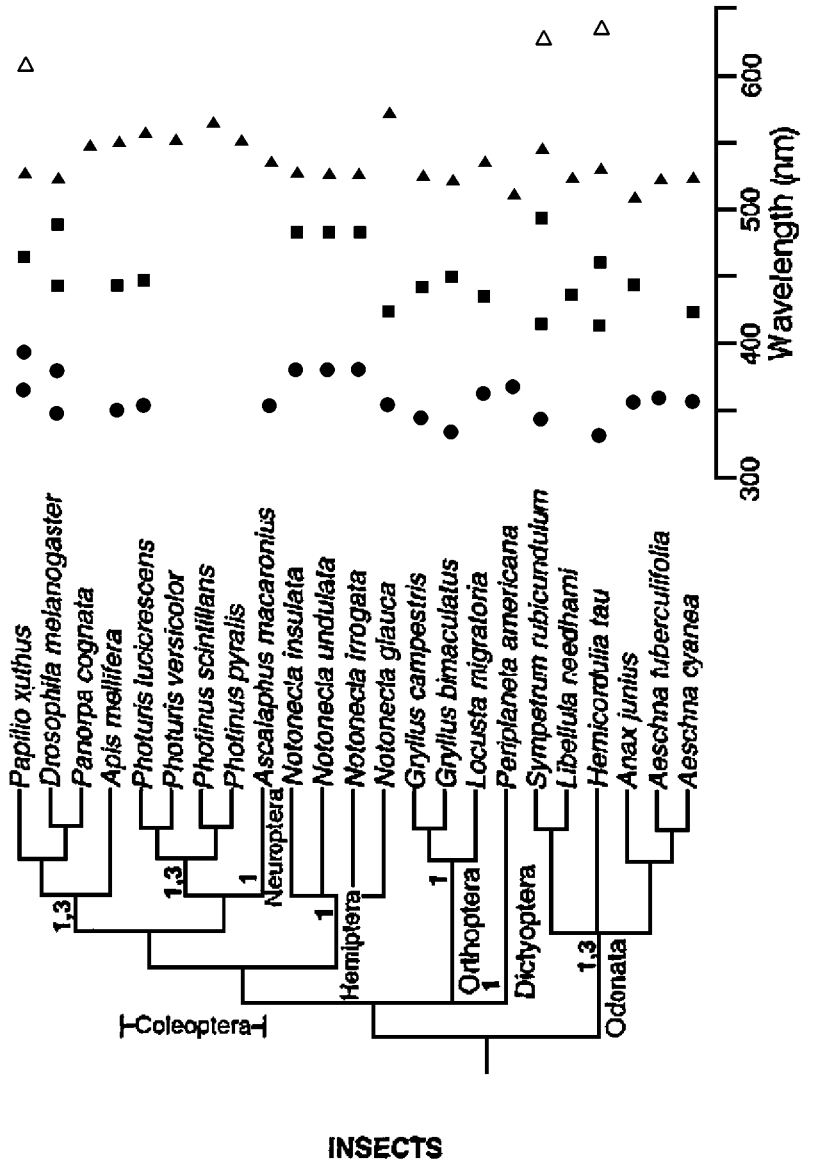


Figure 1 Spectral sensitivity of Insecta and chromophores, superimposed on their phylogeny. Values of maximum sensitivity are shown for each receptor type in each species (for references, see Table 1). Receptor types: circles, UV; squares, blue; solid triangles, green; open triangles, red. Chromophores: 1, 11-*cis* retinal; 3, 11-*cis* 3-hydroxyretinal. For details on phylogeny, see reference 19; for details on chromophores, see references 62 and 141.

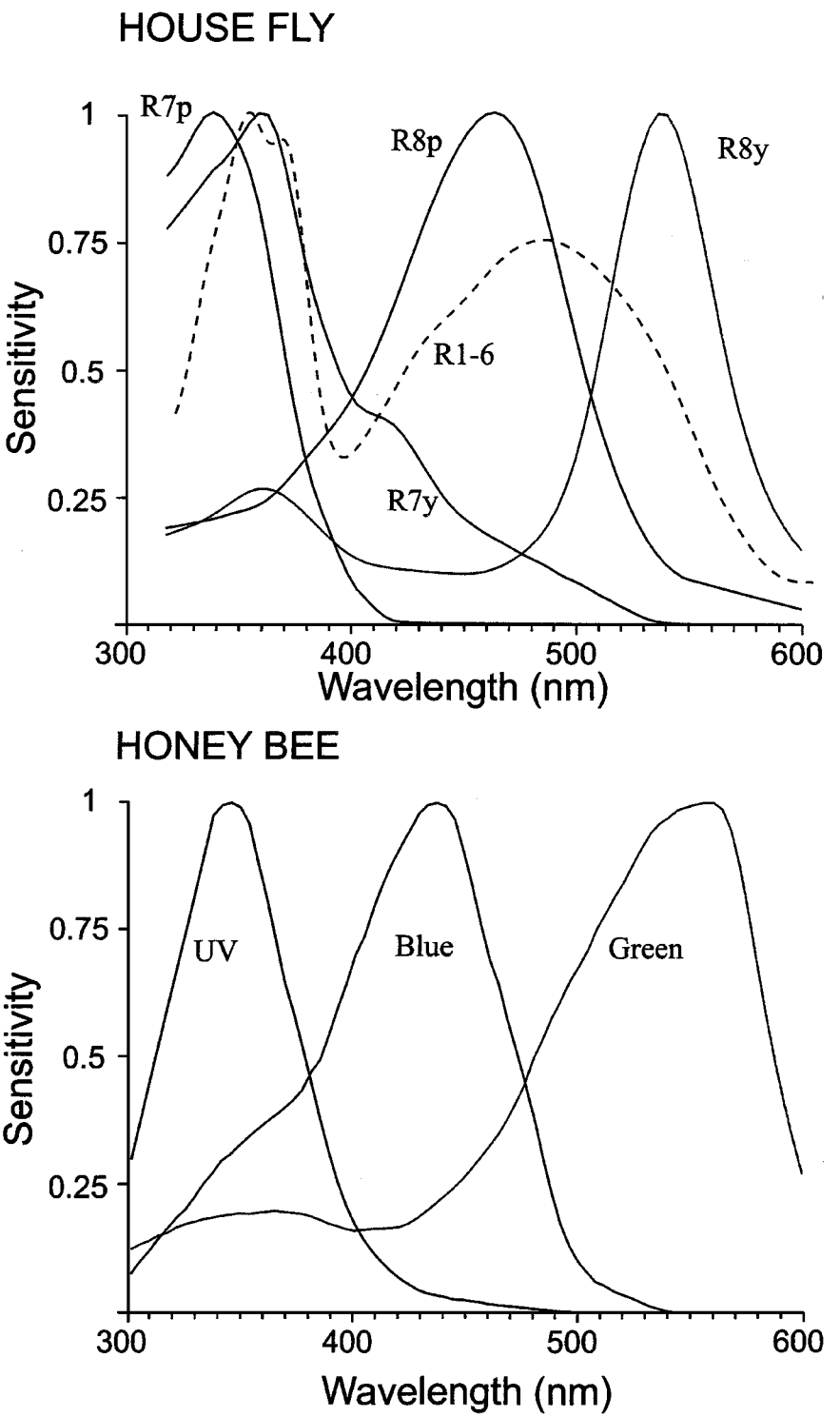
availability of this precursor to insects. Therefore, shifts in the distribution of the biosynthetic precursors to A1 and A3 in plants during the Cretaceous may be one possible explanation for the present-day distribution of A1-and A3-based chromophores within the eyes of insects.

The spatial arrangements of visual pigments, chromophores, screening pigments, and photoreceptor cells in the insect eye also modify spectral sensitivity curves of photoreceptor cells. The structural units of the insect compound eye, the ommatidia, are composed of 8–9 photoreceptor cells that are organized in different ways. Ommatidia are classified according to the structure of their rhabdoms, the photoreceptor cell protrusions that consist of visual pigment-bearing microvillus membranes. Whether rhabdoms are open, fused, or tiered has consequences for the shapes of the photoreceptor cells' spectral sensitivity curves. The rhabdoms of flies are partially open and partially tiered, where the R1–R6 cells each have their own rhabdomere that sees its individual portion of the visual field and the rhabdom of the R7 cell is positioned directly above the R8 (69). Other insects with open rhabdoms are Dermaptera [earwigs (75)], aquatic Hemiptera (26, 99), and some Coleoptera (75).

In fused rhabdoms, rhabdomeres which bear spectrally different photopigments act as lateral filters for one another. This has the effect of keeping spectral sensitivity curves to shapes similar to that of the visual pigment absorption spectrum (143). In the absence of filtering effects (such as in open rhabdoms), the spectral sensitivity curve is broader than the visual pigment absorption spectrum. In tiered rhabdoms, distal photoreceptor cells filter the light that reaches more proximal photoreceptor cells, and the photoreceptor cells' spectral sensitivity curve is again narrowed. Most insects have combinations of fused and tiered rhabdoms [e.g. dragonflies, butterflies, bees, beetles, lacewings, and collembolans (58, 68, 104, 125, 167)].

An example of these effects is illustrated by the fly, in which a blue photostable pigment [a mixture of lutein and zeaxanthin carotenoids with a three-pronged spectrum (69)] in the R7y photoreceptor cell influences the spectral characteristics of the proximal R8 cell (84). In addition to the blue photostable pigment in the receptor cell, a UV-sensitizing pigment, 3-hydroxyretinol—the alcohol form of the A3 chromophore, is also present. This sensitizing pigment absorbs UV light and then transfers the energy of excitation to the visual pigment (which has a λ_{max} of 430 nm). As a consequence of the spectral properties of the blue photostable pigment, the UV-sensitizing pigment, and the visual pigment, the spectral sensitivity curves of these cells are unlike the more typical bee spectral sensitivity curves (Figure 2).

Besides the visual pigments, screening pigments also vary in absorption spectra and in their spatial distribution in the retina. In contrast to the sensitizing pigment of flies, which is thought to be attached to the opsin via hydrogen bonds (69) in the rhabdomere, screening pigments can be found surrounding the rhabdoms (5). To date, there is no systematic study of the distribution of screening pigments (their spectral properties or chemical composition) across insects. This deserves further attention because of increasing evidence that screening pigments and visual pigments can be coordinately modified to enhance different areas of visual performance [i.e. sensitivity vs contrast enhancement (see below)].



The retina of the butterfly *Papilio xuthus* provides us with an example of how screening pigments and visual pigments may be coordinately expressed to produce modified photoreceptor cell spectral sensitivities. Arikawa & Stavenga (5) found different classes of ommatidia distinguished by either yellow or red screening pigments arranged in granules around the rhabdoms in the R3–8 photoreceptor cells. The red pigment is found in threefold as many ommatidia as the yellow, with each class of ommatidium containing spectrally distinct classes of photoreceptor cells. Because the screening pigments selectively absorb short wavelengths, the resulting spectral sensitivities of the photoreceptor cells are slightly red shifted relative to the estimated λ_{max} values of the visual pigments contained within those cells. The red screening pigment is colocalized to ommatidia with red receptors (λ_{max}, 600 nm) containing a visual pigment with $\lambda_{max} = 575$ nm, whereas the yellow screening pigment is colocalized to ommatidia with a green receptor (λ_{max}, 520 nm) and a visual pigment with a peak absorption at 515 nm.

Spectral tuning of visual pigments has been shown to occur through several mechanisms (for a review, see 134). In vertebrate opsins in which a site-directed mutagenesis approach has been applied, almost all of the variation (10–30 nm) in middle- to long-wavelength cone pigment absorption spectra has been accounted for by a mere five to seven specific amino acid substitutions in the chromophore binding pocket of the opsin (6, 110, 149). Vertebrate and insect visual pigments, although structurally and functionally similar, differ in a number of ways. Spectral tuning of vertebrate pigments apparently involves a different subset of amino acid sites than invertebrate pigments (see 20). Owing to the difficulty of heterologously expressing invertebrate pigments (57), much less progress has been made in determining the amino acid sites responsible for spectral tuning of invertebrate pigments.

Britt et al (21) created chimeric opsins by substituting single or multiple TM domains of *Drosophila melanogaster* Rh2 opsin into a *D. melanogaster* Rh1 opsin sequence. These chimeric genes were introduced into a mutant *Drosophila* strain whose native *Rh1* gene contained a deletion. The expression of the chimeric opsins restored normal spectral sensitivity function to the mutant flies. No single TM domain was found to be responsible for the 60-nm difference between Rh1 (480 nm) and Rh2 (420 nm). Exchange of a single Rh1 TM domain for the corresponding Rh2 domain resulted in a 4- to 10-nm blue shift in spectral sensitivity

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Figure 2 Spectral sensitivity of photoreceptor cells in the fly *Musca* (69) and the honey bee *Apis mellifera* (126). In flies, the R1–6 cells form an unusual dual-peaked (UV and green) class, due to the presence of an UV-absorbing sensitizing pigment and a blue-sensitive visual pigment. R7 cells exist in two UV-sensitive classes, p and y. The R7y cell has an especially unusual sensitivity caused by the interaction between a blue absorbing photostable pigment, a UV-sensitizing pigment, and a violet-absorbing opsin. R8 cells fall into another pair of classes, blue (R8p) and green-sensitive (R8y) that are paired with the R7p and R7y cells, respectively. The sensitivity of the R8y cell is explained by taking into account the filtering effects of the overlying R7y cell and a green-sensitive visual pigment. The UV-, blue-, and green-sensitive photoreceptors of the genus *Apis* have spectral sensitivity curves typical of many insects.

for most domains except TM4, in which this exchange resulted in an 11-nm red shift. Replacement of almost all TM domains (TM2–7) was required to convert an Rh1 opsin into an Rh2-like opsin (436 nm).

Unlike the 3 to 5 amino acid residues responsible for tuning the vertebrate red and green cone pigments, the *Drosophila* Rh1 and Rh2 TM domains do not interact in an additive fashion. For example, replacement of only Rh1 TM6 (with an Rh2 TM6) results in a 12-nm blue shift, and replacement of Rh1 TM7 alone results in a 4-nm blue shift. However, replacement of both Rh1 TM6 and TM7 simultaneously results in a 20-nm red shift! Two mechanisms were proposed by Britt et al to account for spectral tuning of the *Drosophila* visual pigments, one involved in large-scale spectral tuning and the other involved in fine-scale tuning, as exemplified by the human red and green cone pigments. While fine tuning is apparently nearly additive in effect (79, 169), coarse tuning occurs in a combinatorial manner, involves many more TM domains, and occurs over a larger evolutionary time scale.

Several studies have used the comparative method to identify potential amino acid substitutions that affect spectral tuning (29, 44, 168). This approach makes use of a phylogeny upon which amino acid substitutions correlated with shifts in λ_{max} can be mapped. Amino acids potentially involved in wavelength regulation have been identified in freshwater crayfish by this method (44). The contributions of these sites to spectral tuning can then be tested by mutagenesis, heterologous expression, and physiological characterization.

DIVERSITY OF VISUAL PIGMENTS, PHYLOGENY, AND ADAPTATION

How plastic is color vision within the insects, and how is variability distributed across their phylogeny? To answer, we started by surveying representatives of different insect orders (Figure 1). These data stem from several different studies with different methods, some of which are noisy and imprecise extracellular recordings. Nevertheless, some trends are apparent. Most insects studied have green receptors maximally sensitive at ~530 nm. In most species, UV receptors ($\lambda_{max} \sim 350$ nm) were also found. There is not a single species in which UV receptors were confirmed absent. For example, in several firefly species in which only green receptors were recorded, the authors themselves concluded that UV and blue receptors exist but were not found (45). Most species also possess blue receptors ($\lambda_{max} \sim 440$ nm), but there are a few cases of confirmed UV-green dichromats (i.e. species in which blue receptors were not found despite intensive search): the owlfly *A. macaronius*, the cockroach *Periplaneta americana*, and some species of ants (see Figures 1 and 3). These species differ widely in lifestyle (*A. macarionius* is a diurnal predator, *P. americana* is a nocturnal scavenger, and of the two formicine ants, one lives in the desert, and the other lives in temperate forests), so there is likely no common adaptive cause for the loss of one receptor type. Red receptors ($\lambda_{max} > 565$ nm) appear several times independently

in the Odonata, the Hymenoptera, the Lepidoptera, and the Coleoptera (Figure 1; Table 1 and references therein). In fact, the Coleoptera contain the insect with the largest λ_{max} value ever recorded, a Glaphyrid beetle (*Amphicoma* sp.) with $\lambda_{max} =$ 630 nm (J Schorn & R Menzel, personal communication). This is intriguing because these scarabaeid beetles (Glaphyridae) prefer to obtain their pollen diet from red, UV-light-absorbing flowers (46). From the data in Figure 1, we conclude that the Devonian ancestor of all pterygote insects likely possessed UV, blue, and green receptors, an interpretation that is supported by molecular biology (see below).

Despite considerable similarities between the receptor sets of different insects, there are also differences that cannot be attributed to measurement error. In one study of the visual pigment absorption spectra, photoreceptor cell spectral sensitivities, and filtering pigment absorption spectra of fireflies, Cronin et al (45) found a remarkable match between the spectral sensitivities of a long-wavelength photoreceptor in the two species of twilight-active fireflies *Photinus pyralis* and *Photinus scintillans* and their bioluminescence emission. This match is produced by the interaction between a long-wavelength visual pigment (which varies by $\sim$10 nm between species) and a pink filtering pigment (the same in both), which acts as a long-pass filter (absorbing short-wavelength light). The resulting photoreceptor spectral sensitivity curve is narrow and nearly identical in shape to the fireflies' emission spectra, which results in a receptor tuned for maximum discrimination of conspecific signals from spectrally broader backgrounds. By contrast, the visual system of the night-active *Photuris versicolor* uses a yellow filtering pigment and a visual pigment ($\lambda_{max} = 545$ nm), which results in a visual system that outperforms the twilight-active species in capturing bioluminescent signals (overall sensitivity), but is predicted to be worse at discriminating conspecific signals from background light. Their study illustrates how altering the visual pigment λ_{max} values or the absorption spectra of the filtering pigments can produce eyes that are either more sensitive (have higher photon capture) or better at discriminating conspecific signals from background light (contrast enhancement).

Unfortunately, this is the only convincing study of adaptive tuning of photoreceptors in insects and it does not involve color vision. Matching of single visual pigments to the illuminant has been well documented in fish (100). Insects do not inhabit the ocean, and so most species live under conditions which are not characterized by a combination of low light intensity and limited spectral range of available light. Many insects are nocturnal or crepuscular. Twilight is blue-shifted relative to daylight and may also contain a relatively strong red component (56), but night light is not substantially different from daylight in spectral terms (100). We now turn to two insect orders in which several species have been studied with comparable methods, the Hymenoptera and the Lepidoptera. The Hymenoptera are interesting because the data for most species are from a single study (126) and because the study species come from a wide variety of habitats, with very different lifestyles and feeding habits (Figure 3). Nevertheless, there is surprisingly little variation in spectral sensitivity. All species, with the exception of ants, possess UV, blue, and green receptors. The few species for which data on UV

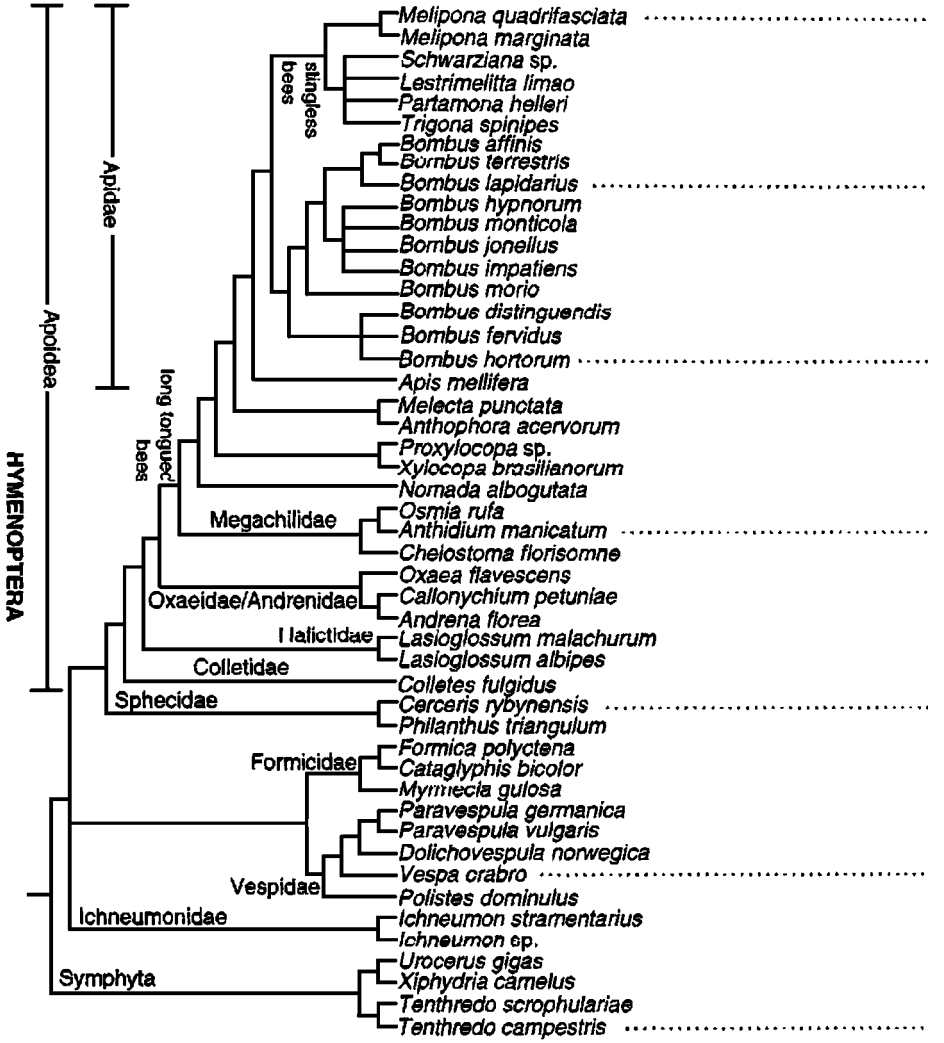

Figure 3 Spectral sensitivity of Hymenoptera, superimposed on their phylogeny, and ecological specializations for which vision is important. Values of maximum sensitivity are shown for each known receptor type in each species (for references, see Table 1). Light habitat or type of activity: A, alpine; D, desert; N, nocturnal activity (in addition to diurnal, which is primary in all these species); TF, tropical forest; TL, temperate lowland. Feeding specializations: GFV, generalist flower visitor; SFV, specialist flower visitor; GCF, generalist carbohydrate forager (flowers, fruits, tree sap, and honeydew); GP, generalist predator; SP, specialist predator; CB, cleptobiotic (*Lestrimelitta limae* obtain its food exclusively by robbing nests of other bees); S, scavenger; PP, phytoparasitism; ZP, zooparasitism (in the latter species, the larvae are parasitic, but the imaginae need to identify appropriate hosts). References for phylogeny include 28, 52, 53, 112, 130, and 138; references for ecological data include 32, 48, 51, 66, 73, 113, 132, 156, 159, 164, and 165.

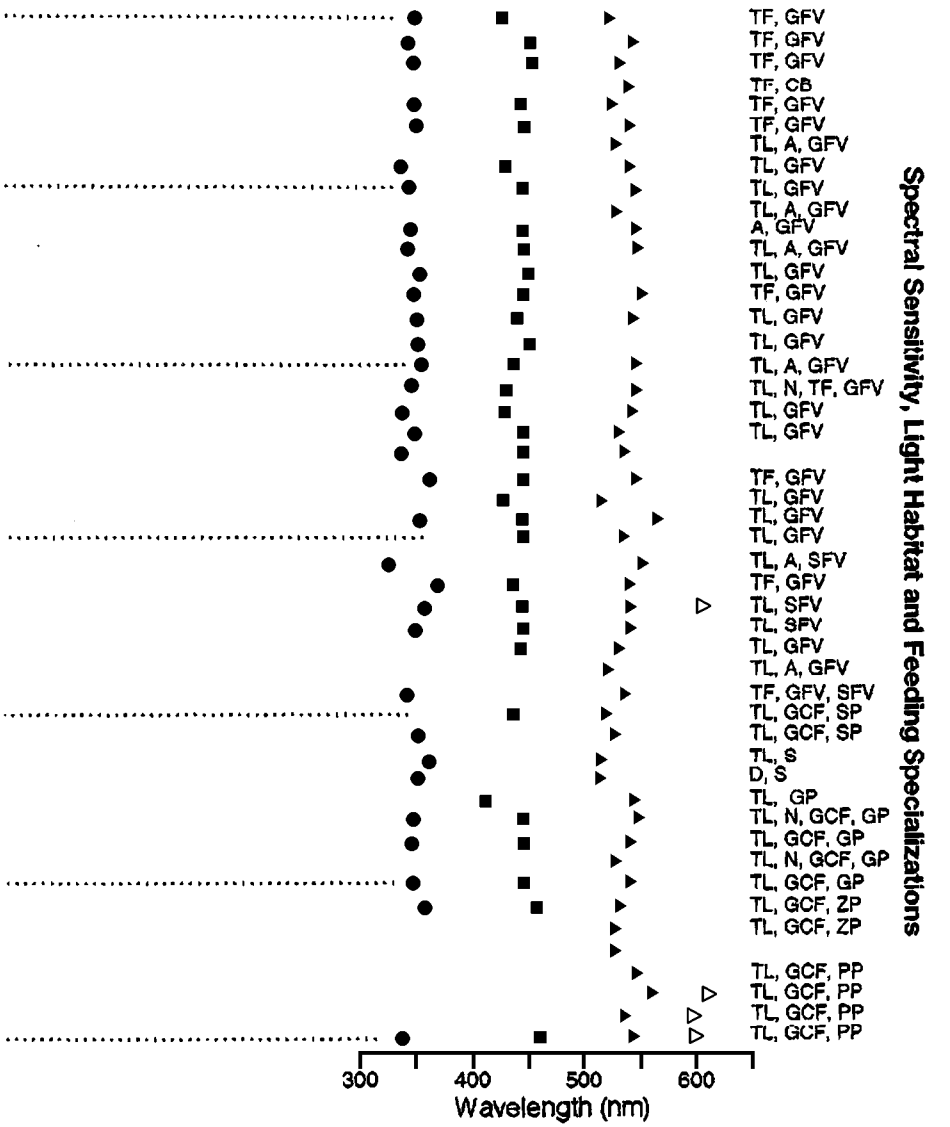

Figure 3 (*Continued*)

and blue receptors are absent, for example, in the Symphyta and Ichneumonidae, presumably represent cases in which the cells exist but were not found. Some species possess additional red receptors, but it is difficult to link their occurrence with ecology. Red receptors were found in three species of Symphyta (thus red receptors were probably present in the ancestor of these species) and one andrenid bee. Even within the obligatorily phytoparasitic Symphyta, there are differences

in lifestyle; whereas *Tenthredo* spp. oviposits on leaves, *Xiphydria camelus* is a wood-boring wasp. *Callonychium petuniae* is a solitary bee that appears to visit purple *Petunia* flowers exclusively (165). Another hymenopteran for which red receptors have been suggested by means of behavioral tests [although unconfirmed by electrophysiological work; (90)] is a desert ant, *Cataglyphis bicolor* (87). It is hard to identify a common selective pressure that might have driven the evolution of red receptors in these species.

The remaining UV-blue-green trichromats include several generalist flower visitors (such as honey bees, stingless bees, and bumble bees) but also a few which specialize on a narrow range of flowers (*Callonychium petuniae*, *Andrena florea*, *Lasioglossum* spp., *Colletes fulgidus*), as well as generalist (*Vespa crabro*) and specialist (*Philanthus triangulum*) predators. They include ground-nesting species (e.g. most bumble bees) as well species that nest in trees (*Apis mellifera*) and termite nests (*Partamona helleri*) or have open nests (*Polistes dominulus*). All species are primarily diurnal, but some are known to forage at night [*Apis mellifera* (156) and *Vespa crabro* (163)]. Some species are obligatorily alpine (e.g. *Bombus monticola*) and so forage in very UV-rich environments, whereas some of the stingless bees may do much of their foraging in dense tropical forests which are relatively poor in the UV range (56). Peitsch et al (126) suggested that the only case of adaptive tuning in the Hymenoptera is a long-wavelength shift in the UV receptor of forest-dwelling stingless bees. An inspection of the λ_{max} values superimposed on the hymenopteran phylogeny does not reveal strong support for this hypothesis, however. The UV receptors of all stingless bee species fall well within the scatter of other apid bees. In conclusion, despite a wide variety of visual-ecological conditions under which the Hymenoptera live, we find little difference in color receptors between most species and, in the few cases in which we do find differences, an adaptive explanation (if any) has yet to be found.

Turning to the Lepidoptera, a similar overall pattern is revealed. Most species appear to possess UV, blue, and green receptors with limited variability in wavelength positioning (Figure 4). There is one intriguing difference in comparison with the Hymenoptera. Whereas only a few species of bees and wasps have red receptors, such receptors are much more common in the Lepidoptera. We used MacClade software to estimate the number of times red receptors ($\lambda_{max} >$ 565 nm) have evolved in Lepidoptera. We included only taxa measured by intracellular recordings, microspectrophotometry, or intracellular optical physiology. We mapped these onto a species phylogeny derived from independent morphological and molecular characters (Figure 5). We caution that this estimate is subject to many potential sources of error, including the robustness of the phylogeny, the physiological data, and the number and distribution of taxa sampled. We note that moths, the most speciose group of the Lepidoptera, are relatively underrepresented in this analysis and that future surveys may reveal additional instances of red receptors. All families of butterflies (excluding skippers) are represented, however. From the available data, we conclude that there is evidence that red receptors evolved at least four times within Lepidoptera: once, in the noctuid moth lineage

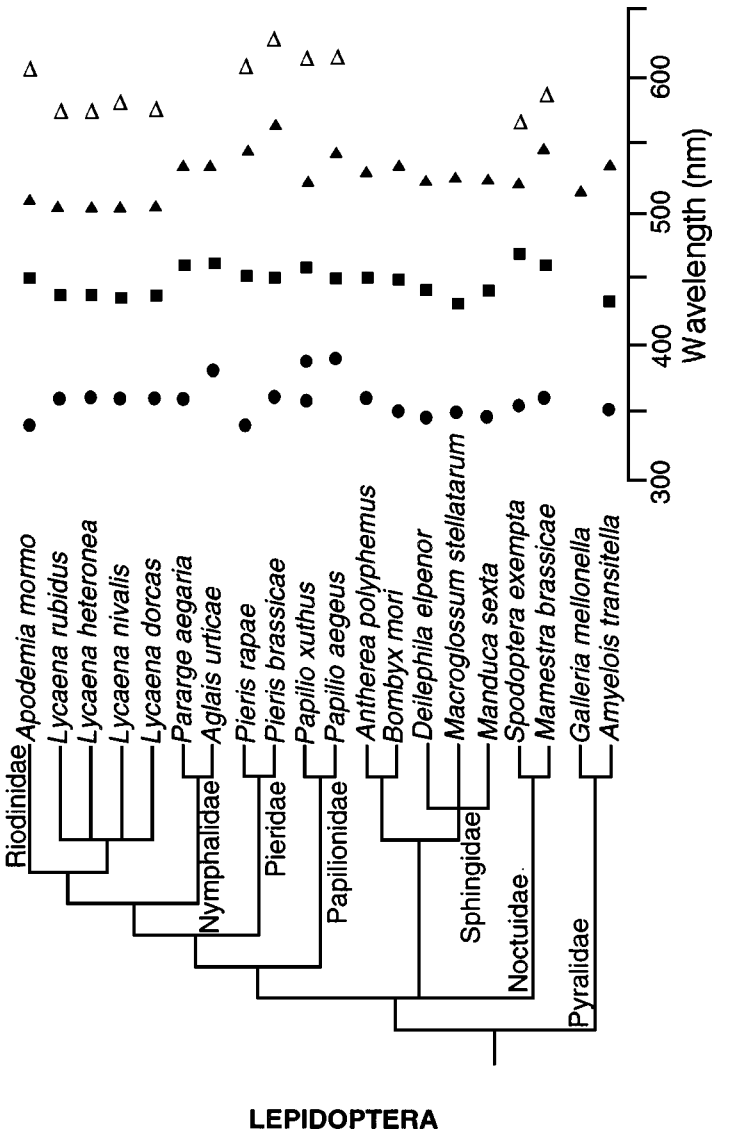

Figure 4 Spectral sensitivity of Lepidoptera, superimposed on their phylogeny. Values of maximum sensitivity are shown for each known receptor type in each species (for references, see Table 1). References for phylogeny include 1, 22, 23, 49, 55, 88, 89, 114, 129, 158.

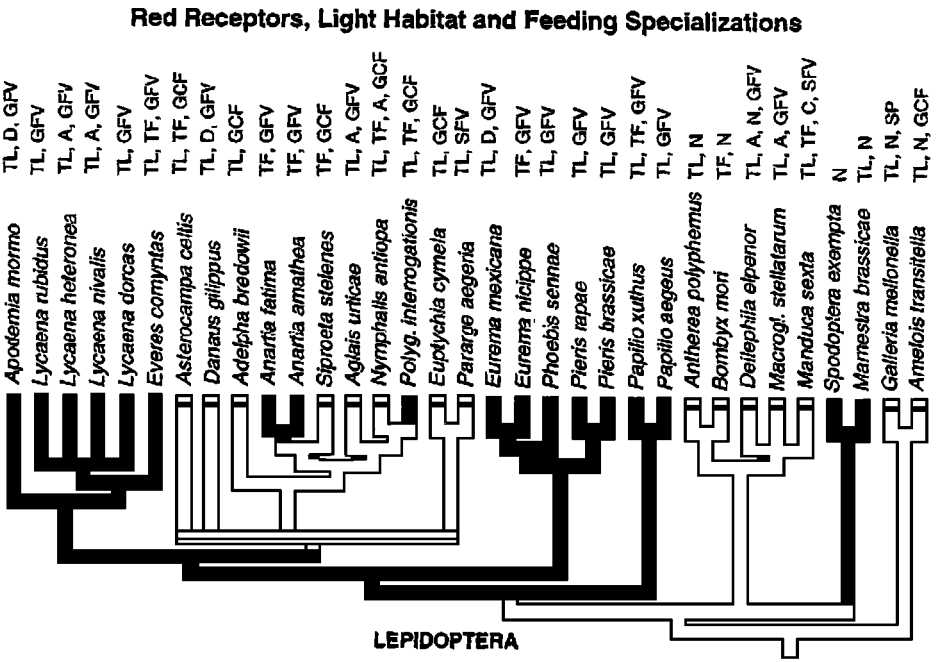

Figure 5 Distribution of red receptors ($\lambda_{max} > 565$ nm) in Lepidoptera, superimposed on their phylogeny, and ecological specializations for which vision is important. Black, branches along which red receptors are hypothesized to have existed based on present-day distributions and parsimony criteria. Light habitat: A, alpine; C, crepuscular activity; D, desert; N nocturnal activity (all butterflies and some moths are diurnal); TF, tropical forest; TL, temperate lowland. Feeding specializations: GFV, generalist flower visitor; SFV, specialist flower visitor; GCF, generalist carbohydrate forager; (tree sap, rotting fruit, honeydew, and dung; SP, specialist predator). For references for phylogeny, see Figure 4 legend. References for ecological data include 42, 43, 131, 140. See also: http://www.npwrc.usgs.gov/resource/distr/lepid/bflyusa/bflyusa.htm.

(a paraphyletic group), once at the base of the butterflies (where there was a major shift toward a diurnal lifestyle), and twice within the Nymphalidae.

We collected behavioral and ecological data on the light habitat and feeding specializations of the lepidopterans included in this analysis to look for possible correlations with the observed pattern of red receptors. The first observation is that a diurnal lifestyle does not seem to be a requirement for having a red receptor. The diurnally active flower-feeding sphingid moth *M. stellatarum*, for instance, lacks red receptors, while the nocturnal *Spodoptera exempta* has them (127). Second, throughout one entire diurnal butterfly family Nymphalidae, the red receptor appears to have been lost, perhaps several times. The only significant change in behavioral ecology in these species is that many of the adults display a preference for tree sap, rotting fruit, and dung (e.g. *Asterocampa celtis*, *Siproeta steneles*, and *Nymphalis antiopa*) over flower nectar. Even this trait, however, is

not tightly correlated with a lack of a red receptor, as *Polygonia interrogationis*, which has a red receptor, shares this unusual feeding preference. Nevertheless, it would be interesting to survey other butterfly species with shifts in adult feeding preferences within a finer-scale phylogenetic framework to see if this trend holds up.

Our review of insect photoreceptor tuning, with the exception of one study of fireflies (45), has found little support for the hypothesis that the environment molds photoreceptor spectral sensitivity. On the contrary, insects with very different lifestyles appear to share similar or identical sets of color receptors, for example in the Hymenoptera. Are these similarities due to an adaptation for an unrecognized common purpose in all of these species? It is more parsimonious to assume that they reflect a constraint (molecular, developmental, or population genetic) that might make it difficult to change spectral sensitivity as easily as a purely adaptionist scenario might suggest (36). The most common change in the receptor arsenal of insects seems to be the evolution of red receptors in addition to the ancestral set of UV, blue, and green receptors. We have not been able to identify a common selective pressure that might underlie the repeated evolution of red receptors or their loss. Therefore, we have to take seriously the possibility that chance evolutionary events play a more important role in sensory ecology than has previously been recognized.

PHOTORECEPTOR ARRAYS, VISUAL ECOLOGY, AND DEVELOPMENT CONSTRAINTS

In many insect eyes, color receptors are not uniformly distributed. An interesting example of how the expression pattern of visual pigments across the eye might be correlated with visual ecology is provided by the butterflies *Lycaena heteronea* and *Lycaena rubidus* (16). Both species possess the same set of four photopigments with $\lambda_{max} = 360$, 437, 500, and 568 nm, but the distribution across the retina differs between species. *L. heteronea* has a blue wing color and possesses blue receptors in its ventral eye, in addition to the three other types. In *L. rubidus*, the wings reflect both in the UV and red; in this species, blue receptors are absent in the ventral eye. Thus, expression of the blue pigment gene in the ventral eye might be driven by the occurrence of blue sexual signals in *L. heteronea*. Furthermore, there is a sexually dimorphic distribution of color receptors in the dorsal eye. While males of both species are UV-blue dichromats, females have additional red receptors. This was interpreted as an adaptation to detect the red foliage of the host plants, which the females use for oviposition. However, these plants are probably viewed with the ventral eye, which contains red receptors in both sexes of the two species; hence the adaptive significance of the sexual differences in the dorsal eye remains uncertain.

In honey bees, eye regions used for color vision (the frontal-ventral eye in workers) contain several receptor types (106), but there are other regions which seem specifically adapted for certain tasks and which often contain only reduced

receptor sets. The dorsal regions of many insects lack green receptors for example. Honey bee drones have only UV and blue receptors in that region (106), whereas in the owlfly (63) and several species of flies (144), even the blue receptors are absent. Some workers suggested that the UV receptor might be optimally suited to detect the open sky or to detect small objects (such as flying mates) against the bright sky (105). Whether this interpretation holds must be quantitatively determined by modeling.

Honey bees use green receptors for several motion-related tasks (95, 106). Could this be an adaptation by which the motion-perceptual channel is best matched to the prevailing background of most habitats inhabited by bees—green leaves? The green receptor is certainly more suited for this task than the other bee receptors, but wavelength tuning could be improved; leaves reflect at longer wavelengths than those at which most insect (including bee) green receptors absorb (36).

It would be informative to know whether the ancestral ommatidium contained all three color receptor types, with specialized eye regions and fewer receptor types arising secondarily, perhaps as adaptations to specific visual tasks. Unfortunately, there are too few studies with enough fine-scale physiological or molecular mapping of the visual pigments expressed within the ommatidium (see e.g. 92, 93) to map on a phylogeny of insects and thus to answer this question comparatively. While there is much evidence of dorsal-ventral differences in receptor distributions (12, 16), there is no clear picture of how quickly these differences evolve. Comparative in situ hybridization or immunohistochemistry data would be extremely useful.

So far we have considered the hypothesis that observed physiological differences in different parts of the eye (such as the dorsal-ventral regions of various insects) may be adaptations for specific visual tasks. Another possibility needs consideration, namely that regional differences in opsin expression are merely side effects of "upstream" developmental-patterning processes. Dorsal-ventral patterning genes, transcription factors that regulate the expression of many downstream genes, are known for many structures (limbs, eyes, etc). To be able to explore this possibility, that opsin expression is linked to developmental constraints, more fine-scale molecular characterization of opsin expression patterns and the developmental mechanisms that regulate those expression patterns is needed. If the developmental processes that regulate opsin expression are relatively easy to modify genetically, we might expect that eyes might be more easily modified by natural selection. If opsin expression is regulated by processes that are not easily modified, then the observed patterns of opsin expression might be a direct reflection of such developmental constraints. One potentially fruitful approach to measuring the amount of developmental plasticity available for creating variant eyes would be to perform selection experiments on *Drosophila melanogaster*, along the lines of those described by Polaczyk et al (128), who selected for flies with differing numbers of R7 cells.

Drosophila melanogaster has five retina-specific opsins, Rh1 (122, 171) and Rh3–6 (40, 78, 115, 171), and one ocellar (simple eye)-specific opsin, Rh2. Rh1 is expressed in the R1–R6 photoreceptor cells in all ommatidia, whereas opsins

Rh3–6 have a more complex pattern of expression. The R7 cells express either of two UV opsins, Rh3 or Rh4, in an apparently cell-autonomous way (41). By contrast, the R8 cell expresses either a blue or a green opsin, Rh5 or Rh6, in a process that is directly dependent on the opsin-expressing state of the overlying R7 cell (41). When the Rh3 opsin is expressed in the R7 cell of a particular ommatidium, the Rh5 opsin is always coexpressed in the R8 cell (40, 123). Similarly, when the Rh4 opsin is expressed in the R7 cell of an ommatidium, the Rh6 opsin is always coexpressed in the R8 cell. Removal of R7 cells in mutant flies disrupts Rh5 expression and increases Rh6-expressing cells, whereas removal of R8 cells has no effect on the generation of both Rh3- and Rh4-expressing R7 cells (41). Phylogenetically, this particular pattern of coordinated expression of opsins is likely to be a recent event, because Rh3 and Rh4 appear to be the result of a gene duplication event so far detected only in Diptera (see Figure 6).

MOLECULAR PHYLOGENY OF INSECT VISUAL PIGMENTS

To understand how visual pigments in insects have been modified over evolutionary time, it is informative to evaluate the phylogeny of their opsins. This exercise has the added advantage of providing us with a semi-independent means of verifying the common ancestry of various spectral classes of photoreceptors. To this end, we compared the amino acid sequences of the opsins of 54 species of arthropods, as well as different opsins found within the same animal species. The basis of such an analysis is that proteins that are most similar are grouped together, with the nodes of the tree representing (hypothetical) ancestral opsins (65). What immediately emerges from this analysis is that insect opsins fall into three major clades (Figure 6), which confirms the view that UV, blue, and green visual pigments arose early in the evolution of insects. In addition, *Drosophila melanogaster* expresses a pair of duplicated blue-green opsin genes (Rh1 and Rh2) that have no known homologs in other surveyed insects. Moreover, the λ_{max} value (480 nm) of the Rh1 opsin, which is expressed in the majority of photoreceptor cells (R1–6) in the *Drosophila* retina, is unlike the sensitivity of most photoreceptor classes in insects (cf the 420-nm ocellar-specific Rh2 opsin). This clade of opsins appears at the base of the opsin gene family tree and has apparently persisted a long time in the *Drosophila* genome. We have to consider the possibility that some insects that have not been surveyed may contain a visual pigment with a similar sensitivity. In this case, we would have to modify our view of the early insect eye as possibly including a fourth major spectral class, as well as the possibility that it has been lost many times within insects.

When we consider the pattern of opsin gene duplication in the butterfly genus *Papilio*, we find evidence supporting the view developed earlier, that within various insect orders, red receptors have evolved more than once. There are four long-wavelength opsins reported for *Papilio glaucus* (20) that cluster with a long wavelength moth opsin cloned from *Manduca sexta* (31). If the observed distribution

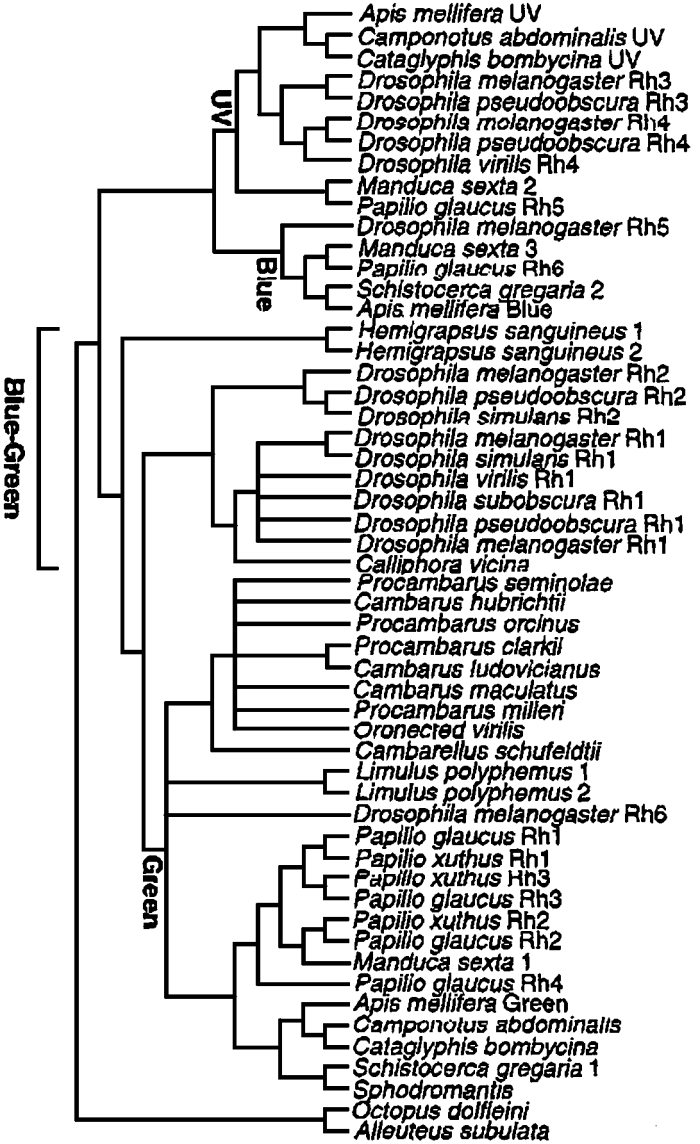

Figure 6 Molecular phylogeny of arthropod opsins based on a parsimony analysis of amino acid sequences. Nodes with bootstrap values <50% have been collapsed. Seven arthropod taxa are represented: Chelicerata, Crustacea, Orthoptera, Mantodea, Hymenoptera, Diptera, and Lepidoptera. Several distinct opsin cDNAs or genes from the same organism have been isolated (e.g. three from *Apis mellifera* and *Manduca sexta*, and six each from *Drosophila melanogaster* and *Papilio glaucus*). Most opsins cluster together into three major clades, UV, blue, and green. The *D. melanogaster* Rh1 and Rh 2 opsins form a separate clade that branches off near a basal clade of *Hemigrapsus sanguineus* opsins, with similar sensitivity. Several gene duplications are evident in *D. melanogaster, P. glaucus, H. sanguineus*, and *Limulus polyphemus*. For references on phylogeny, physiology, and sequences, see 20.

of red receptors was not caused by independently evolved red-sensitive visual pigments (from ancestral green-sensitive visual pigments), then we would expect some of these opsins, which have been recently localized to red- or green-sensitive photoreceptor cells in the butterfly retina (see 85), to be more closely related to some of the hymenopteran opsin sequences under the alternative hypothesis that red-sensitive visual pigments had a single origin early in the evolution of insects. The data, so far, suggest independent origins.

On a finer scale, one way of directly testing this would be to isolate opsins from taxa apparently not bearing a red receptor (such as within specific nymphalid butterflies), as well as from moth taxa bearing apparently independently evolved red receptors, and analyze the pattern of gene duplication in relation to other known insect opsins. We would expect to see a pattern of gene loss near the base of the nymphalid family, followed by a pair of duplications within some nymphalid lineages, as well as an independent duplication in the moth taxa bearing red receptors (such as *Spodoptera*). We expect that future molecular surveys will be extremely useful in narrowing the timeframe within which novel visual pigment sensitivities evolve.

EVIDENCE FOR VARIANCE BETWEEN INDIVIDUALS OF THE SAME SPECIES

Individual variation is the substrate for evolution. It provides populations with the genetic resources to respond to changing environments and colonize new habitats. Lack of such variation in populations does not mean that the traits are not adaptive, however. A trait that is strongly selected for is likely to sweep through the population and replace other variants. As scientists sampling static population data, snapshots in time and space, we may not be in the right place at the right time to witness such selective sweeps in action. But studying such processes is important because they offer us the opportunity to study the conditions under which a trait may be adaptive. One phenotype may be favored in one photic environment while another phenotype is favored in another. Many physiologists, however, treat phenotypic variation as noise, which needs to be eliminated by averaging large numbers of experimental data points from different animals. This practice is sometimes legitimate. Physiological data are often so noisy that extracting information is not possible without some averaging. Strong deviations from expectation can indicate less-than-ideal experimental conditions. However, much valuable information on the phenotypic variation in natural populations may have been lost through such averaging!

Is it possible that the reason for much of the conservatism in arthropod color receptors is that there is no variation between individuals in the same species, or has such variation gone unnoticed through the (largely unavoidable) practice of averaging physiological measurements? Many scientists have worked on the color receptors of honey bees, for instance, and their results have differed both within

and between studies. Much of the debate about these differences has focused on the possible contributions of artifacts or the differences between measurements by different electrophysiological methods (109). Certainly, both of these can add noise to the measurements, but, unfortunately, the possibility that interindividual variance may also contribute has not been considered. Notably, honey bee opsins have been cloned in recent years (10, 29, 152), and allelic variation has been reported (152). However, no functional studies exist demonstrating that these alleles have any effect on honey bee spectral sensitivities.

In some vertebrates, by contrast, such variation exists and has been well studied, for example in guppies (3) and primates (47, 142). To our knowledge, only one other published study on insects (besides 152) reports intraspecific variation between opsin sequences. Ayala et al (8) sampled five Rh3 alleles from each of four species in the *D. melanogaster* subgroup and three alleles from *D. pseudoobscura*. Only one of the five surveyed species contained a single amino acid polymorphism. In the butterfly *Papilio glaucus*, intraspecific amino acid variation has also been observed (A Briscoe, personal observation). Again, we cannot be sure whether any of these naturally occurring variants differs in its spectral sensitivities. Clearly, we need more data and a combination of approaches, molecular and physiological, to test the physiological consequences of visual pigment allelic variation.

Humans provide us with a further example of population-level differences in visual pigment allelic variation. A single amino acid polymorphism at position 180 in the red opsin protein exists in humans, which produces a red receptor maximally absorbing at 557 nm. Among Caucasians, 62% have serine at this position, whereas 38% have alanine, which produces a red receptor maximally sensitive at 552 nm. Males, who carry only one copy of this gene because it is located on the X chromosome and who have Ser at residue 180, have a higher sensitivity to red light (47). In African Americans, the percentage of individuals carrying the serine-180 allele is 80%, whereas the frequency of the alanine-180 allele is 20%. In Japanese, the percentages are 84% and 16%, respectively (47). Are these population differences likely to be adaptive? We prefer the hypothesis that these differences are caused by genetic drift. Similarly, Ayala et al (8) concluded that the single-amino acid polymorphism they detected in *Drosophila* spp. was evolving by selectively neutral processes.

Another example from human color vision provides us a more clearly nonadaptive pattern of variation. On the tiny Pacific island of Pingelap, a part of the Federated States of Micronesia, ∼1 in 20 of the 3000 Pingelapese is totally colorblind; the eyes in these individuals have only rods. This is the result of a bottleneck that occurred after a typhoon hit the island in 1775, when the population then of almost 1000 was reduced to only 20 survivors, one of whom was the king. After several generations, the population returned to its pretyphoon level (133). Unfortunately, the king was carrier of the gene responsible for color blindness, so that today one-third of the population carries the recessive gene that is responsible for this defect, and ∼5% of the population is phenotypically color blind (150). In worldwide populations the frequency of this defect is ∼1 in 50,000. The cause of this form of colorblindness has recently been identified as a mutation in a subunit of

a photoreceptor-specific ion channel (150). It is, of course, possible that adaptive between-population differences in visual systems do exist. In stickleback fish, for instance, McDonald & Hawryshyn (103) were able to correlate interpopulation differences with the light environment. We merely wish to caution that not all differences between populations may be adaptive. Random evolutionary processes may also explain some of the differences between species, but studies to explore this possibility in insects are few.

Often, although the performance of one phenotype may be found to be better than another at a given task executed in the lab, this may not have any impact on the fitness of the individual. To return to the human red receptor polymorphism above, would we expect that an individual with a red receptor with a λ_{max} of 557 nm will have more surviving offspring than someone with a red receptor with λ_{max} of 552 nm, even if it turns out that the person with the 557-nm λ_{max} is slightly better at detecting red fruit? Probably not. Even the color-blind Pingelapese are able to detect and identify ripe fruits (133). Humans may be underconstrained in evolutionary terms, but we do not know how limiting the visuo-ecological conditions are for most other species either. They remain to be determined empirically. If the color vision systems of animals are not sitting on narrow adaptive peaks, or if multiple sensory channels can be used because of redundancy of information, even strong deviations from the wild-type phentoype may not be selected against.

Trichromatic marmosets perform better at detecting orange fruit against a dappled foliage background than their dichromatic conspecifics (27). If trichromacy were completely favored over dichromacy by natural selection, we might expect that the single locus encoding the marmoset red and green receptors would duplicate, and all members of the population would be trichromats. Instead, a single locus with several alleles and a large fraction of the population (males and homozygous females) persist as dichromats not only in marmosets but in related species of New World monkeys. Whether this occurs because of an unrecognized advantage of dichromats over trichromats at a task not related to frugivory remains to be tested. Without additional data on other visual tasks essential for survival and reproduction, we also have to consider the possibility that the advantage of trichromats at detecting fruit is so small under natural conditions that it is irrelevant to fitness. The "take-home" message is that, in addition to measuring the performance of visual systems in relation to specific tasks, we need fitness tests under natural conditions.

COLOR CODING BEYOND THE RECEPTOR LEVEL

Menzel (105) suggested that color vision evolved from wavelength-selective behavior, a more primitive form of processing input from different spectral-receptor types. Wavelength-selective behavior occurs when specific behavioral responses are triggered by specific configurations of signals from the photoreceptors (65); for example, sea anemones retract their tentacles when exposed to UV light but bend them towards visible light (105). This behavior has no plasticity; it cannot be

altered by learning. In such cases, it is therefore parsimonious to assume that the motor circuits are connected to rather unprocessed output from the visual periphery in a hard-wired fashion. Color vision, conversely, allows animals to process stimulus intensity and chromaticity independently. This ability has been demonstrated in most insects tested so far, i.e. numerous species of Hymenoptera (35, 87, 106), Diptera (59, 153), and Lepidoptera (157). Color vision and numerous types of wavelength-specific behavior exist side by side in bees and other insects (65, 105). It is likely that wavelength-specific behavior indeed predated the evolution of color vision, because numerous invertebrates without elaborate vision have more than a single visual pigment, and they respond differently to different wavelengths (105). But can Menzel's hypothesis be tested by phylogenetic methods? Do arthropods retain some of the neural machinery in conjunction with visual pigments from their wormlike ancestors? What changes did this circuitry undergo as animals evolved complex eyes and color vision, and possibly adapted to different visual ecological niches?

Unfortunately, our understanding of neuronal processing of the information provided by insect color receptors is limited to fewer species than our understanding of the receptors themselves. Physiological data about color-coding neurons are very hard to get, and even if we have the data, they tell us very little about how (and if) these neurons are actually used in color vision. We present information on color coding only when comparisons between species allow the deduction of evolutionary implications, that is, when data from several species are available.

The basic architecture of the optic lobes in malacostracan crustaceans and insects is extremely similar and was likely present in a common ancestor (121). The visual information is passed from the receptor level to three successive ganglia, called lamina, medulla, and lobula. Of the 8 or 9 photoreceptors present in each ommatidium, 6 or 7 terminate in the lamina (short visual fibers), whereas 1–3 project to the lobula (long visual fibers) (120). Based on comparisons between fruit flies, honey bees, locusts, and crayfish, Osorio & Bacon concluded that the ancestral *bauplan* of these animals involved long-wavelength sensitivity (blue-green) in the short visual fibers and at least one long visual fiber with UV sensitivity. There are variations on this theme, however: In dragonflies, for example, the long visual fibers respond to either green or violet light, but the UV receptors project only into the lamina (104).

Across insect orders, one function of short visual fibers with long-wave (green) sensitivity is the input to motion perception, for example in flies (69, 81), locusts (119), and bees (95). In flies, color vision is apparently mediated entirely by long visual fibers with sensitivities in the UV, blue, and green wavelengths (59, 153), so the two pathways (color and motion vision) are entirely separate even on the receptor level. But in other insects, such as bees, long-wave (green) receptors apparently serve both motion vision and color vision. Here, both the long and short visual fibers contribute to color vision (106).

The internal wiring of the lamina, as well as lamina-medulla connections, is highly conserved across insects from different orders and even across many

crustaceans (120). Small interspecific differences in neuronal circuitry do exist, however. Their relationship to visual ecology has been demonstrated (94, 118) but not in relation to color vision. One widespread type of identified neurons that appears to be central in color vision is the large monopolar cells, which relay the information from the photoreceptor cells to the medulla. Some of these cells appear to simply amplify the unprocessed signals from particular photoreceptors (50), while others sum inputs from two or three spectral receptor types, possibly to form the initial stage of a brightness-coding system (106).

One essential prerequisite for color vision is the presence of color opponent coding, by means of neurons that compare signals from different color receptor types. Unfortunately, there are too few studies of such neurons to reveal any evolutionary patterns. Tonic color opponent neurons with antagonistic inputs from visible and UV light have been found in the medulla in bees (82) and locusts (119). In butterflies, various types of color-opponent neurons have been identified in the protocerebrum (151). This reveals only that there is similarity in insect visual systems, as well as plasticity—not more. Unfortunately, we also lack clear hypotheses about how color coding should differ between species living in different visual conditions.

Behavioral studies on color coding also reveal much less information than one would hope for. In all nine species of trichromatic Hymenoptera so far tested, color discrimination data can be best explained when one assumes that color is coded by using two-color opponent mechanisms (9, 35). In all of these species, the assumption of a brightness dimension either does not improve, or it actually worsened, the precision with which color discrimination could be predicted (35). This indicates a common (and ancestral) strategy of color-coding in these species. Unfortunately, these studies were not designed to identify the precise nature of the underlying color-coding mechanisms. When statistics are applied rigorously, it is impossible to distinguish between numerous possible combinations of color opponent mechanisms, and thus it is also impossible to distinguish between species (35). New behavioral studies along the lines pursued in primate color vision (86) are necessary. Optimality considerations, however, predict that the quality of discrimination of natural objects is rather insensitive to the precise nature of opponent coding (with bee receptors at the input level), so long as the mechanisms are orthogonal (33).

Flies of the genus *Lucilia* appear to differ from bees in terms of color coding. While color discrimination in bees improves smoothly with increasing color difference between two stimuli (11), these flies lump colors in three broad categories each about 100 nm wide, and they treat all colors as either "same" or "different" to a training stimulus, depending on whether they fall inside the same category (153). Whether this type of color coding constitutes a particular adaptation in *Lucilia* spp. or it extends to all flies remains to be shown. Again, such differences between orders show that there is some plasticity in insect color coding, but we cannot conclude whether these differences are related to lifestyle.

A BIOGEOGRAPHICAL APPROACH TO STUDYING EVOLUTION OF VISION-RELATED TRAITS

Comparisons between orders may be too coarse grained to reveal the extent to which insect color coding may be modified by ecological requirements. To identify a visual trait that might reveal a pattern of adaptation to the visual environment, we evaluated the innate floral color preferences of different bumble bee species and populations of the same species (38). We hypothesized that evolutionary changes of such preferences require only changes in the relative synaptic efficiency between neurons that code information from the color receptors. Color preferences might respond more strongly to the profitability of local flowers than the λ_{max} values of the receptors.

The color preferences of naïve honey bees and the amounts of nectar offered by flowers with different colors exhibited a good correlation in a nature reserve near Berlin, Germany (61). Honey bees most strongly preferred violet (bee UV-blue) and blue (bee blue) colors, which were associated with high nectar rewards. This pattern may not be unique to Germany; a similar association of flower color with reward was found in Israel (108). But a correlation, however strong, never proves causality. To show that color preferences respond evolutionarily to floral offerings, a comparison of closely related bee species (or populations of the same species) that live in habitats in which the associations of floral colors with rewards are different must be made.

Seven species of bumble bees from three subgenera were tested: four from central Europe (*Bombus terrestris terrestris, B. lucorum, B. pratorum*, and *B. lapidarius*), two from Asia (*B. ignitus* and *B. hypocrita*), and one from North America (*B. occidentalis*). All species showed a strong preference for shades in the violet-blue range. This preference may represent the ancestral state of these species (38). Besides this, however, *B. occidentalis* exhibited the strongest preference for red of all mainland bumble bee populations examined, a result which is interesting because this species forages heavily from western American hummingbird flowers (39). Because this preference is not shared with the other species, it might be an adaptation that is unique to *B. occidentalis*.

In *B. terrestris*, several populations were tested: *B. terrestris terrestris* from Holland, *B. terrestris terrestris* from Germany, *B. terrestris dalmatinus* from Israel, *B. terrestris dalmatinus* from Rhodes; *B. terrestris sassaricus* from Sardinia, *B. terrestris xanthopus* from Corsica, and *B. terrestris canariensis* from the Canary Islands. Because island populations are often small, the effects of genetic drift are more likely to manifest themselves than in large mainland populations (2). Some island populations of *B. terrestris* are distinct in coat color and on the molecular genetic level from each other and from the mainland population. By contrast, the entire mainland population, which stretches all through central, southern, and eastern Europe, appears to be genetically more homogeneous (162).

Correspondingly, no strong differences in color preferences were found between the mainland *B. terrestris* populations. All showed the same type of strong preference for violet-blue shades as the other species described above. Remarkably,

some island populations show an additional red preference (Figure 7). In *B. t. sassaricus*, this preference is stronger than that for blue colors in some colonies, and it is highly significant in all colonies. In *B. t. canariensis*, four of five colonies showed a high preference of red over yellow and orange. The adaptive significance of such red preference is not easy to understand. Some species of red, UV-absorbing, and pollen-rich flowers exist in the Mediterranean basin, particularly the eastern part, with the highest concentration in Israel (46). In Israel, however, bumble bees do not show red preference, and these flowers appear to be predominantly visited by beetles (46). Some red blooming species exist in Sardinia too but in low numbers, and their value for bumble bees is unclear. The Canary Islands harbor several orange-red flower species (155). These are probably relics of a Tertiary flora, and some seem strongly adapted to bird pollination. They do not appear to be utilized by bees (155). Thus, we are left with the observation that flower color preferences are clearly variable within *B. terrestris* but cannot be easily correlated with differences in local flower colors. The possibility that genetic drift has produced the color preferences in some island populations thus deserves consideration. To explore this possibility further, it will be necessary to sample the local floral market in more detail and to test whether red preference might simply evolve in some island populations because it is not selected against. A useful approach will be to exploit between-colony differences in preferences, to measure their actual impact on foraging performance and fitness.

Finally, the observed patterns of floral color preferences within bumble bees suggest that the receptor level might be worth looking at again. Could it be that some species of bumble bees (such as *B. occidentalis*) or some island populations of *B. terrestris* have red receptors (or are polymorphic for red alleles)? Clearly, the observation of red preference itself cannot be taken as evidence for the existence of red receptors (39). But red flowers do take substantially longer to detect than those of other colors for bees without red receptors (38), so that the evolution of red receptors might be favored in species whose range overlaps with that of red flowers. Assuming that physiological work might indeed reveal the existence of red receptors in bumble bees with red preference, there might be two evolutionary paths toward such receptors in bees. In large populations, red receptors might only become fixed in case of a strong selective advantage, such as in bees that already exploit red hummingbird flowers. Conversely, if the fitness advantage conferred by red receptors is comparatively small, new mutants that carry such receptors might be eliminated by genetic drift with very high probability. In case of such a minor adaptive advantage, red receptors might spread through only relatively small populations, such as those on islands.

CONCLUSION

Several decades of searching for evolutionary adaptations in insect color vision have borne relatively little fruit. Rather, we find a bewildering pattern of ecologically unexplained differences in the ways different insects see color and, in other

cases, similarities where ecology would predict difference. This might mean that we have not yet identified the important selective pressures. Before we try new adaptive explanations, we wish to issue a warning: Given too many hypotheses and the fact that most insects have multiple photoreceptors, there is a high danger of finding a correlation between physiology and at least one hypothesis, just by chance. It will also be fairly easy to fall into the trap of interpreting any mismatch as a tradeoff between two (or more) different visual demands. There is no easy way around these problems, except to use rigorous evolutionary analyses and to consider alternatives to adaptation.

If we find similarities in sensory systems between different species despite predicted differences, the conclusion is not necessarily that we need different predictions. Instead, the most parsimonious conclusion is that the respective animals have the sensory systems they do because they have inherited them from a common ancestor and that constraints have kept them from optimally adapting to their environment. Such constraints might be molecular, so that changing spectral sensitivity in insects might require an improbable sequence of mutation events. There could also be inertia related to population genetics. The probability of a new mutation spreading through a population is proportional to its adaptive value and inversely proportional to population size. If an adaptive change must be based on several small evolutionary steps each of which is selectively neutral, then a new mutation which might confer such a small step is likely to be lost by genetic drift. Adaptation, then, is not an inevitable process that follows naturally from any type of selective pressure, however marginal its strength.

One problem in visual ecology is that we do not know the adaptive value of any sensory trait. Physiologists have largely treated theoretical optimality arguments as identical to adaptive value, rather than measuring adaptiveness directly by fitness tests. The shapes of the adaptive peaks of insect color vision systems are unknown, and thus it is hard to predict the strength of selection or the influence of genetic drift. To test this possibility directly, it will be necessary to measure heritable variation between individuals of the same species and to exploit this variation for fitness tests under natural conditions. We urge readers to take on such studies to understand the diversity of color vision systems (and other sensory and behavioral abilities) used by insects and other animals.

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TABLE 1 Insect spectral sensitivity data—values of maximum sensitivity of each receptor cell[a]

Taxon	λ_{max} values	Methods[b]	Reference(s)
ODONATA			
Sympetrum rubicundulum	340, 410, 490, 540, 620	IntCell	104
Hemicordulia tau	330, 410, 460, 525, 630	IntCell	166
Aeschna cyanea	356, 420, 519	IntCell	7
A. tuberculifolia	358, 501	IntCell	30
Libellula needhami	430, 519	IntCell	74
Anax junius	354, 442, 503	IntCell	30
DICTYOPTERA			
Periplaneta americana	365, 505	IntCell, ERG	116, 124
ORTHOPTERA			
Gryllus bimaculatus	332, 445, 515	IntCell	170
G. campestris	340, 439, 520	IntCell	170
Locusta migratoria	360, 430, 530	IntCell	154
HEMIPTERA			
Notonecta undulata	375, 475, 520	ERG	11
N. isulata	375, 475, 520	ERG	11
N. glauca	350, 420, 567	IntCell	24
N. irrogata	375, 475, 520	ERG	11
NEUROPTERA			
Ascalaphus macaronius	350, 530	ERG, IntCell	63, 124
COLEOPTERA			
Coccinella septempunctata	360–380, 510–530	ERG	97
Carabus nemoralis	348, 430, 500, 620	ERG	71
C. auratus	348, 430, 500, 620	ERG	71
Photinus pyralis	P545[c]	MSP	45
P. scintillans	P557	MSP	45
Photuris lucicrescens	350, 440, 550	ERG	91
Ph. versicolor	P545	MSP	45
HYMENOPTERA			
Melipona quadrifasciata	356, 428, 520 [349, 426, 525]	IntCell	126
M. marginata	340, 450, 540	IntCell	126
Schwarziana sp.	343, 440, 528 [348, 453, 523]	IntCell	126
Lestrimelitta limao	536	IntCell	126
Partamona helleri	347, 444, 521	IntCell	37
Trigona spinipes	340, 440, 536 [349, 445, 533]	IntCell	126
Bombus affinis	525	SpecPupil	17
B. terrestris	328, 428, 536 [336, 428, 529]	IntCell	126

(*Continued*)

TABLE 1 (*Continued*)

Taxon	λ_{max} values	Methods[b]	Reference(s)
B. lapidarius	332, 432, 544 [341, 445, 540]	IntCell	126
B. hypnorum	524	IntCell	126
B. monticola	336, 440, 544 [346, 445, 535]	IntCell	126
B. jonellus	336, 432, 544 [341, 445, 542]	IntCell	126
B. impatiens	352, 450	SpecPupil	17
B. morio	352, 428, 548 [349, 445, 539]	IntCell	126
B. distinguendis	350, 440, 540	ERG	38
B. fervidus	350, 450	SpecPupil	17
B. hortorum	353, 436, 544	IntCell	111
Apis mellifera, f	344, 436, 544 [346, 430, 540]	IntCell	126
A. mellifera, m	328, 436, 532 [346, 445, 529]	IntCell	126
Melecta punctata	336, 428, 540	IntCell	126
Anthophora acervorum	348, 428, 528 [348, 445, 524]	IntCell	126
Proxylocopa sp.	312, 424, 532 [338, 445, 524]	IntCell	126
Xylocopa brasilianorum	360, 428, 544 [362, 445, 538]	IntCell	126
Nomada albogutata	428, 512	IntCell	126
Osmia rufa	344, 432, 560 [354, 445, 553]	IntCell	126
Anthidium manicatum	324, 440, 532 [356, 445, 531]	IntCell	126
Chelostoma florisomne	324, 548	IntCell	126
Oxaea flavescens	370, 435, 536	IntCell	126
Callonychium petuniae	360, 404, 536, 600 [356, 445, 531, 593]	IntCell	126
Andrena florea	340, 412, 536 [348, 445, 529]	IntCell	126
Lasioglossum malachurum	442, 528	IntCell	126
L. albipes	516	IntCell	126
Colletes fulgidus	340, 532	IntCell	126
Cerceris rybynensis, f	436, 516	IntCell	126
C. rybynensis, m	528	IntCell	126
Philanthus triangulum	344, 444, 524 [352, 445, 529]	IntCell	126

TABLE 1 (*Continued*)

Taxon	λ_{max} values	Methods[b]	Reference(s)
Formica polyctena	360, 510	ERG	107
Cataglyphis bicolor	350, 510	ERG	117, 124
Myrmecia gulosa	412, 540	IntCell	96
Paravespula germanica	336, 432, 544 [347, 445, 534]	IntCell	126
P. vulgaris	336, 432, 536 [346, 445, 531]	IntCell	126
Dolichovespula norwegica	448, 524	IntCell	126
Vespa crabro, f	336, 436, 536 [346, 445, 529]	IntCell	126
V. crabro, m	542	IntCell	126
Polistes dominulus	352, 452, 528 [358, 457, 527]	IntCell	126
Ichenumon stramentrius	524	IntCell	126
Ichneumon sp.	524	IntCell	126
Urocerus gigas	542	IntCell	126
Xiphydria camelus	556, 604	IntCell	126
Tenthredo scrophulariae	532, 592		
Tenthredo campestris	328, 464, 540, 596 [337, 458, 537, 602]	IntCell	126
MECOPTERA			
Panorpa cognata	540	ERG	25
DIPTERA			
Calliphora erythrocephala	350, 490	IntCell, ERG	124
C. vicinia	344, 344, 490,	SpecPupil	18
Dimecoenia spinosa	480	SpecPupil	18
Toxomerus marginatus	450	SpecPupil	18
Allograpta obliqua	460	SpecPupil	18
Drosophila melanogaster	345, 370, 440, 480, 520	SpecPupil, MSP	18, 135
Cyrtodiopsis dalmanni	360, 450, 490	ERG	25
Bibio marci	520	ERG	25
Bibio sp.	340	ERG	83
Phaenicia sericata	480	IntCell	102
Musca domestica	335, 430, 460, 490, 520	IntCell	69
Eristalis tenax	350, 450, 520	IntCell	77
Eeristalis arbustorum	450	SpecPupil	18
Syrphus sp.	440	SpecPupil	18
Chlorops sp.	480	SpecPupil	18
Haemotopata sp.	530	ERG	83

(*Continued*)

TABLE 1 (*Continued*)

Taxon	λ_{max} values	Methods[b]	Reference(s)
LEPIDOPTERA			
Papilionidae			
Papilio aegeus	390, 450, 540, 610	IntCell	101
P. xuthus	360, 390, 460, 520, 600	ERG, IntCell	4, 54
P. protenor	420, 460, 520,	ERG	54
P. bianor	420, 460, 520, 580	ERG	54
P. machaon	380, 460, 520, 580,	ERG	54
P. maackii	380, 460, 520, 580	ERG	54
Atrophaneura alcinous	420, 460, 520, 600	ERG	54
Graphium sarpedon	380, 460, 560, 600	ERG	54
Pieridae			
Colias erate	400, 520, 560	ERG	54
Gonepteryx aspasia	380, 460, 560, 620	ERG	54
Eurema mexicana	Red receptor[d]	SpecPupil	13
Eurema nicippe	Red receptor	SpecPupil	13
Phoebis senna	Red receptor	SpecPupil	13
Pieris rapae	340, 450, 540, 600	IntCell	13, 80
P. brassicae	360, 450–460, 560, 620	IntCell, ERG	124, 146
P. melete	400, 480, 540, 600	ERG	54
Nymphalidae			
Heliconius erato	370, 470, 570	ERG	148
H. numata	390, 460, 540	ERG	147
H. sara	370, 470, 550	ERG	148
Fabriciana adippe	380, 460, 520, 580	ERG	54
Argyronome ruslana	380, 440, 560, 620	ERG	54
Danaus gilippus	P360, P470, P550	MSP	G Bernard, personal communication
Asterocampa celtis	No red receptor	SpecPupil	13
Adelpha bredowii	No red receptor	SpecPupil	13
Anartia fatima	Red receptor	SpecPupil	13
A. amathea	Red receptor	SpecPupil	13
Siproeta steneles	No red receptor	SpecPupil	13
Vanessa cardui	P530	MSP	13
Polygonia c-album	380, 520, 560, 620	ERG	54
P. interrogationis	Red receptor	SpecPupil	13
Inachis io	No red receptor	SpecPupil	G Bernard, personal communication
Aglais urticae	380, 460, 530	ERG	146
Nymphalis vau-album	No red receptor	SpecPupil	13

TABLE 1 (*Continued*)

Taxon	λ_{max} values	Methods[b]	Reference(s)
N. antiopa	No red receptor	SpecPupil	13
N. xanthomelas	380, 460, 500, 560	ERG	54
Minois dryas	380, 460, 520	ERG	54
Neope goschkevitschii	380, 460, 520	ERG	54
Pararge aegaria	360, 460, 530	IntCell, ERG	124
Euptychia cymela	No red receptor	SpecPupil	13
Riodinidae			
Apodemia mormo	340, 450, 505, 600	SpecPupil, MSP	G Bernard, personal communication
Lycaenidae			
Celastrina argiolus	380, 440, 560	ERG	54
Pseudozizeeria maho	400, 520, 580	ERG	54
Lycaena rubidus	P360, P437, P500, P568	MSP	16
L. heteronea	P360, P437, P500, P568	MSP	16
L. dorcas	P360, P437, P500, P568	MSP	16
L.nivalis	P360, P437, P500, P575	MSP	16
L. phlaeas	400, 540, 600	ERG	54
Everes comyntas	Red receptor	SpecPupil	13
Hesperiidae			
Ochlodes venata	380, 460, 520	ERG	54
Parnara guttata	380, 460, 520	ERG	54
Pyralidae			
Amelois transitella	350, 430, 530	SpecPupil, ERG	15, 54
Galleria mellonella	P510	MSP	64
Sphingidae			
Deilephila elpenor	P345, P440, P520	MSP	67, 72, 136, 139
Manduca sexta	P345, P440, P520–530	MSP,ERG	93, 160
Marumba spershius	460, 540, 600	ERG	54
Ampelophaga rubiginosa	460, 540, 580	ERG	54
Callambulyx tatarinovii	380, 460, 540, 580	ERG	54
Macroglossum stellatarum	348, 430, 500	ERG	71
Bombycidae			
Bombyx mori	350, 450, 530	IntCell, larval	80

(*Continued*)

TABLE 1 (*Continued*)

Taxon	λ_{max} values	Methods[b]	Reference(s)
Noctuidae			
Spodoptera exempta	355, 465, 515, 560	MSP, ERG	92
Mamestra brassicae	360, 460, 540, 580	IntCell, larval	80
Anadevidia peponis	420, 460, 500	ERG	54
Saturniidae			
Actias artemis aliena	380, 460, 540, 580	ERG	54
Samia cynthia ricini	380, 400, 480, 520, 540	ERG	54
Antherea polyphemus	P360, P450, P525	MSP	93
Hepialidae			
Phassus excrescens	380, 460, 520, 580	ERG	54
Epicopeiidae			
Epicopeia hainesii	380, 420, 500	ERG	54
Geometridae			
Arichanna gaschkevitchii	360, 500, 540	ERG	54

[a]Peitsch et al (126) used the absolute maxima of the measurements as their λ_{max} values. Since, however, these measurements are noisy, a better estimate of a receptor's true wavelength value of maximum sensitivity can be obtained by fitting a pigment template to the actual measurement curve. In this way, all measurement values contribute to the determination of the λ_{max}. We created templates by the method of Stavenga et al (145) for all λ_{max} values from 320 to 630 nm (in 1-nm steps), and we calculated the sum of all squared deviations of all of these templates from each actual measurement over the range of 300–700 nm. This procedure could be applied only to those species for which a figure was available in reference 126. We determined the λ_{max} value for each measured curve by using the λ_{max} of the template with the lowest sum of squared deviations (least-square-fit method). The results are shown in brackets below the values given by Peitsch et al (126).

[b]IntCell, intracellular recordings; SpecPupil, intracellular optical recordings; ERG, electroretinograms; MSP, microspectrophotometry.

[c]P denotes a visual pigment absorption spectrum maximum; all other entries are photoreceptor cell spectral sensitivities.

[d]Red receptor, $\lambda_{max} > 565$ nm; no red receptor, $\lambda_{max} < 565$ nm.

NOTE: Red receptors recorded by ERG may not be due to the presence of a red-sensitive visual pigment; they may be due to screening pigments, selective shielding by overlying short wavelength visual pigments, or coexpressed photostable pigments.

LITERATURE CITED

1. Ackery PR. 1984. Systematic and faunistic studies on butterflies. In *The Biology of Butterflies*, ed. R VaneWright, PR Ackery, pp. 9–21. Princeton, NJ: Princeton Univ. Press
2. Adkison MD. 1995. Population differentiation in Pacific salmon: local adaptation, genetic drift, or the environment. *Can. J. Fish. Aquat. Sci.* 52:2762–77
3. Archer SN, Endler JA, Lythgoe JN, Partridge JC. 1987. Visual pigment polymorphism in the guppy *Poecilia reticulata*. *Vis. Res.* 27:1243–52
4. Arikawa K, Inokuma K, Eguchi E. 1987. Pentachromatic visual system in a butterfly. *Naturwissenschaften* 74:297–98

5. Arikawa K, Stavenga D. 1997. Random array of colour filters in the eyes of butterflies. *J. Exp. Biol.* 200:2501–6
6. Asenjo AB, Rim J, Oprian DD. 1994. Molecular determinants of human red/green color discrimination. *Neuron* 12: 1131–38
7. Autrum H, Kolb G. 1968. Spektrale Empfindlichkeit einzelner Sehzellen der Aeschniden. *Z. Vergl. Physiol.* 60:450–77
8. Ayala FJ, Chang BSW, Hartl DL. 1993. Molecular evolution of the Rh3 gene in *Drosophila*. *Genetica* 92:23–32
9. Backhaus W. 1991. Color opponent coding in the visual system of the honeybee. *Vis. Res.* 31:1381–97
10. Bellingham J, Wilkie SE, Morris AG, Bowmaker JK, Hunt DM. 1997. Characterization of the ultraviolet-sensitive opsin gene in the honey bee, *Apis mellifera*. *Eur. J. Biochem.* 243:775–81
11. Bennett RR, Ruck P. 1970. Spectral sensitivities of dark- and light-adapted *Notonecta* compound eyes. *J. Insect Physiol.* 16:83–88
12. Bennett RR, White RH, Meadows J. 1997. Regional specialization in the eye of the sphingid moth *Manduca sexta*: blue sensitivity of the ventral retina. *Vis. Neurosci.* 14:523–26
13. Bernard GD. 1979. Red-absorbing visual pigments of butterflies. *Science* 203:1125–27
14. Bernard GD. 1983. Bleaching of rhabdoms in eyes of intact butterflies. *Science* 219:69–71
15. Bernard GD, Owens ED, Hurley AV. 1984. Intracellular optical physiology of the eye of the pyralid moth *Amyelois*. *J. Exp. Zool.* 229:173–87
16. Bernard GD, Remington CL. 1991. Color vision in *Lycaena* butterflies: spectral tuning of receptor arrays in relation to behavioral ecology. *Proc. Natl. Acad. Sci. USA* 88:2783–87
17. Bernard GD, Stavenga DG. 1978. Spectral sensitivities of retinular cells measured in intact, living bumblebees by an optical method. *Naturwissenschaften* 65:442–43
18. Bernard GD, Stavenga DG. 1979. Spectral sensitivities of retinular cells measured in intact living flies by an optical method. *J. Comp. Physiol. A* 134:95–107
19. Boudreaux H. 1979. *Arthropod Phylogeny with Special Reference to Insects.* New York: Wiley & Sons, 320 pp.
20. Briscoe AD. 2000. Six opsins from the butterfly *Papilio glaucus*: molecular phylogenetic evidence for paralogous origins of red-sensitive visual pigments in insects. *J. Mol. Evol.* 51:110–21
21. Britt SG, Feiler R, Kirschfeld K, Zuker CS. 1993. Spectral tuning of rhodopsin and metarhodopsin in vivo. *Neuron* 11:29–39
22. Brower AVZ. 2000. Phylogenetic relationships among the Nymphalidae (Lepidoptera) inferred from partial sequences of the *wingless* gene. *Proc. R. Soc. London Ser. B.* 267:1201–11
23. Brower AVZ, DeSalle R. 1998. Patterns of mitochondrial versus nuclear DNA sequence divergence among nymphalid butterflies: the utility of *wingless* as a source of characters for phylogenetic inference. *Insect Mol. Biol.* 7:73–82
24. Bruckmoser P. 1968. Die spektrale empfindlichkeit einzelner sehzellen des rückenschwimmers *Notonecta glauca* L. (Heteroptera). *Z. Vergl. Physiol.* 59:187–204
25. Burkhart D, De LaMotte I. 1972. Electrophysiological studies on the eyes of Diptera, Mecoptera and Hymenoptera. In *Information Processing in the Visual Systems of Arthropods*, ed. R Wehner, pp. 137–45. Berlin: Springer-Verlag
26. Burton P, Stockhammer R. 1969. Electron microscopic studies of the compound eye of the Toadbug, *Gelastocoris oculatus*. *J. Morphol.* 127:233–58
27. Caine NG, Mundy NI. 2000. Demonstration of a foraging advantage for trichromatic marmosets (*Callithrix geoffroyi*)

dependent on food colour. *Proc. R. Soc. London Ser. B.* 267:439–44
28. Cameron SA. 1993. Multiple origins of advanced eusociality in bees inferred from mitochondrial DNA sequences. *Proc. Natl. Acad. Sci. USA* 90:8687–91
29. Chang BSW, Crandall KA, Carulli JP, Hartl DL. 1995. Opsin phylogeny and evolution: a model for blue shifts in wavelength regulation. *Mol. Phylogenet. Evol.* 4:31–44
30. Chappell RL, DeVoe RD. 1975. Action spectra and chromatic mechanisms of cells in the median ocelli of dragonflies. *J. Gen. Physiol.* 65(4):399–419
31. Chase MR, Bennett RR, White RH. 1997. Three opsin-encoding cDNAs from the compound eye of *Manduca sexta*. *J. Exp. Biol.* 200:2469–78
32. Chinery M. 1984. *Insekten Mitteleuropas*. Hamburg, Germany: Parey, 444 pp.
33. Chittka L. 1996. Optimal sets of colour receptors and opponent processes for coding of natural objects in insect vision. *J. Theor. Biol.* 181:179–96
34. Chittka L. 1997. Bee color vision is optimal for coding flower colors, but flower colors are not optimal for being coded—why? *Isr. J. Plant Sci.* 45:115–27
35. Chittka L, Beier W, Hertel H, Steinmann E, Menzel R. 1992. Opponent colour coding is a universal strategy to evaluate the photoreceptor inputs in Hymenoptera. *J. Comp. Physiol. A* 170:545–63
36. Chittka L, Briscoe A. 2000. Why sensory ecology needs to become more evolutionary—insect color vision as a case in point. In *Ecology of Sensing*, ed. FG Barth, A Schmid. Berlin: Springer-Verlag
37. Chittka L, Schorn J, de Souza JM, Ventura DF, Camargo JMF. 1997. The nest entrance signal of the Amazonian bees *Partamona pearsoni*—a case where insects design their own flight targets. *Proc. Int. Colloq. Social Insects*, ed. VE Kipyakov. 3–4:107–16. St. Petersburg, Russia: Socium
38. Chittka L, Spaethe J, Schmidt A, Hickelsberger A. 2001. Adaptation, constraint, and chance in the evolution of flower color and pollinator color vision. In *Cognitive Ecology of Pollination*, ed. L Chittka, J Thomson. Cambridge, UK: Cambridge Univ. Press
39. Chittka L, Waser NM. 1997. Why red flowers are not invisible for bees. *Isr. J. Plant Sci.* 45:169–83
40. Chou W-H, Hall KJ, Wilson DB, Wideman CL, Townson SM, et al. 1996. Identification of a novel *Drosophila* opsin reveals specific patterning of the R7 and R8 photoreceptor cells. *Neuron* 11:1101–15
41. Chou W-H, Huber A, Bentrop J, Schulz S, Schwab K, et al. 1999. Patterning of the R7 and R8 photoreceptor cells of *Drosophila*: evidence for induced and default cell-fate specification. *Development* 126:607–16
42. Common I. 1972. *Butterflies of Australia*. Sydney: Angus & Robertson. 498 pp.
43. Comstock J. 1927. *Butterflies of California: A Popular Guide to a Knowledge of the Butterflies of California, Embracing All of the 477 Species and Varieties at Present Recorded for the State*. Los Angeles, CA: Comstock. 334 pp.
44. Crandall KA, Cronin TW. 1997. The molecular evolution of visual pigments of freshwater crayfishes (Decapoda: Cambaridae). *J. Mol. Evol.* 45:524–34
45. Cronin TW, Jarvilehto M, Weckstrom M, Lall AB. 2000. Tuning of photoreceptor spectral sensitivity in fireflies (Coleoptera:Lampyridae). *J. Comp. Physiol. A* 186:1–12
46. Dafni A, Bernhardt P, Shmida A, Ivri Y, Greenbaum S, et al. 1990. Red bowl-shaped flowers: convergence for beetle pollination in the Mediterranean region. *Isr. J. Bot.* 39:81–92
47. Deeb SS, Motulsky AG. 1996. Molecular genetics of human color vision. *Behav. Genet.* 26:195–207

48. Degen K. 1991. *Experimente zur Farbunterscheidung von wespen (Paravespula vulgaris) in der Dämmerung*. LA-Arb. TH Darmst.
49. deJong R, VaneWright RI, Ackery PR. 1996. The higher classification of butterflies (Lepidoptera): problems and prospects. *Entomol. Scand.* 27:65–101
50. de Souza J, Hertel H, Ventura DF, Menzel R. 1992. Response properties of stained monopolar cells in the honeybee lamina. *J. Comp. Physiol. A* 170:267–74
51. Dobson HEM. 1987. Role of flower and pollen aromas in host-plant recognition by solitary bees. *Oecologia* 72:618–23
52. Dowton M, Austin AD. 1994. Molecular phylogeny of the insect order Hymenoptera: apocritan relationships. *Proc. Natl. Acad. Sci. USA* 91:9911–15
53. Dowton M, Austin AD. 1997. Evidence for AT-transversion bias in wasp (Hymenoptera: Symphyta) mitochondrial genes and its implications for the origin of parasitism. *J. Mol. Evol.* 44:398–405
54. Eguchi E, Watanabe K, Hariyama T, Yamamoto K. 1982. A comparison of electrophysiologically determined spectral responses in 35 species of Lepidoptera. *J. Insect Physiol.* 28:675–82
55. Ehrlich PR, Ehrlich AH. 1967. The phenetic relationships of the butterflies. I. Adult taxonomy and the nonspecificity hypothesis. *Syst. Zool.* 16:301–17
56. Endler JA. 1993. The color of light in forests and its implications. *Ecol. Monogr.* 63:1–27
57. Engels A, Reichert H, Gehring WJ, Gärtner W. 2000. Functional expression of a locust visual pigment in transgenic *Drosophila melanogaster*. *Eur. J. Biochem.* 267:1917–22
58. Friedrich M, Rambold I, Melzer RR. 1996. The early stages of ommatidial development in the flour beetle *Tribolium castaneum* (Coleoptera: Tenebrionidae). *Dev. Genes Evol.* 206:136–46
59. Fukushi T. 1994. Colour perception of single and mixed monochromatic lights in the blowfly *Lucilia cuprina*. *J. Comp. Physiol.* 175:15–22
60. Gärtner W, Ullrich D, Vogt K. 1991. Quantum yield of CHAPSO-solubilized rhodopsin and 3-hydroxyretinal containing bovine opsin. *Photochem. Photobiol.* 54:1047–55
61. Giurfa M, Núñez J, Chittka L, Menzel R. 1995. Colour preferences of flower-naive honeybees. *J. Comp. Physiol. A* 177:247–59
62. Gleadall IG, Hariyama T, Tsukahara Y. 1989. The visual pigment chromophores in the retina of insect compound eyes, with special reference to the Coleoptera. *J. Insect Physiol.* 35:787–95
63. Gogala M. 1967. Die spektrale Empfindlichkeit der Doppelaugen von *Ascalaphus macaronius* Scop. (Neuroptera, Ascalaphidae). *Z. Vergl. Physiol.* 57:232–43
64. Goldman LJ, Barnes SN, Goldsmith TH. 1975. Microspectrophotometry of rhodopsin and metarhodopsin in the moth *Galleria*. *J. Gen. Physiol.* 66:383–404
65. Goldsmith TH. 1990. Optimization, constraint, and history in the evolution of eyes. *Q. Rev. Biol.* 65:281–322
66. Hagen E. 1990. *Hummeln: bestimmen, ansiedeln, vermehren, schützen*. Augsburg, Germany: Naturbuch Verlag. 320 pp.
67. Hamdorf K, Höglund G, Langer H. 1971. Mikrophotometrische Untersuchungen an der Retinula des Nachtschmetterlings *Deilphila elpenor*. *Verh. Dtsch. Zool. Ges.* 65:276–80
68. Hammerle B, Kolb G. 1996. Retinal ultrastructure of the dorsal eye region of *Pararge aegeria* (Linne) (Lepidoptera: Satyridae). *Int. J. Insect Morphol. Embryol.* 25:305–15
69. Hardie RC. 1986. The photoreceptor array of the dipteran retina. *Trends Neurosci.* 9:419–23
70. Hariyama T, Tsukahara Y, Meyer-Rochow VB. 1993. Spectral responses, including a

UV-sensitive cell type, in the eye of the isopod *Ligia exotica*. *Naturwissenschaften* 80:233–35

71. Hasselmann E-M. 1962. Über die relative spektrale Empfindlichkeit von Käfer—und Schmetterlingsaugen bei verschiedenen Helligkeiten. *Zool. Jahrb. Physiol.* 69:537–76
72. Höglund G, Hamdorf K, Langer H, Paulsen R, Schwemer J. 1973. The photopigments in an insect retina. In *Biochemistry and Physiology of Visual Pigments*, ed. H Langer, pp. 167–80. Berlin/Heidelberg/New York: Springer-Verlag
73. Hölldobler B, Wilson EO. 1990. *The Ants*. Berlin: Springer-Verlag. 733 pp.
74. Horridge GA. 1969. Unit studies on the retina of dragonflies. *Z. Vergl. Physiol.* 62:1–37
75. Horridge GA, Giddings D. 1971. Movement on dark-light adaptation in beetles eyes of the neuropteran type. *Proc. R. Soc. London Ser. B* 179:73–85
76. Horridge GA, Marcelja L, Jahnke R. 1984. Colour vision in butterflies. I. Single colour experiments. *J. Comp. Physiol. A* 155:529–42
77. Horridge GA, Mimura K, Tsukahara Y. 1975. Fly photoreceptors. II. Spectral and polarized light sensitivity in the drone fly *Eristalis*. *Proc. R. Soc. London Ser. B* 190:225–37
78. Huber A, Schulz S, Bentrop J, Groell C, Wolfrum U, et al. 1997. Molecular cloning of *Drosophila* Rh6 rhodopsin: the visual pigment of a subset of R8 photoreceptor cells. *FEBS Lett.* 406:6–10
79. Hunt DM, Fitzgibbon J, Slobodyanuk SJ, Bowmaker JK. 1996. Spectral tuning and molecular evolution of rod visual pigments in the species flock of cottoid fish in Lake Baikal. *Vis. Res.* 36:1217–24
80. Ichikawa T, Tateda H. 1982. Distribution of color receptors in the larval eyes of four species of Lepidoptera. *J. Comp. Physiol.* 149:317–24
81. Kaiser W, Liske E. 1974. Optomotor reactions of stationary flying bees during stimulation with spectral light. *J. Comp. Physiol.* 89:391–408
82. Kien J, Menzel R. 1977. Chromatic properties of interneurons in the optic lobes of the bee. II. Narrow band and colour opponent neurons. *J. Comp. Physiol. A* 113:35–53
83. Kirschfeld K. 1986. Activation of visual pigment chromophore structure and function. In *Life Sciences Research Report, 34: The Molecular Mechanism of Photoreception; Dahlem Workshop*, ed. H Stieve, pp. 31–50. Berlin: Springer-Verlag
84. Kirschfeld K, Feiler R, Franceschini N. 1978. Photo-stable pigment within rhabdomere of fly photoreceptors no. 7. *J. Comp. Physiol.* 125:275–84
85. Kitamoto J, Sakamoto K, Ozaki K, Mishina Y, Arikawa K. 1998. Two visual pigments in a singe photoreceptor cell: identification and histological localization of three mRNAs encoding visual pigment opsins in the retina of the butterfly *Papilio xuthus*. *J. Exp. Biol.* 201:1255–61
86. Krauskopf J, Williams DR, Heeley DW. 1982. Cardinal directions of color space. *Vis. Res.* 22:1123–31
87. Kretz R. 1979. A behavioural analysis of colour vision in the ant *Cataglyphis bicolor* (Formicidae, Hymenoptera). *J. Comp. Physiol. A* 131:217–33
88. Kristensen N. 1976. Remarks on the family-level phylogeny of butterflies (Insecta, Lepidoptera, Rhopalocera). *Z. Zool. Syst. Evol.* 14:25–33
89. Kristensen N, Skalski A. 1998. Phylogeny and palaeontology. In *Lepidoptera, Moths and Butterflies*, ed. NP Kristensen, 1:7–25. Berlin: Walterde Gruyter
90. Labhart T. 1986. The electrophysiology of photoreceptors in different eye regions of the desert ant, *Cataglyphis bicolor*. *J. Comp. Physiol. A* 158:1–7
91. Lall AB, Lord ET, Trouth CO. 1982. Vision in the firefly *Photuris lucicrescens*

(Coleoptera: Lampyridae): spectral sensitivity and selective adaptation in the compound eye. *J. Comp. Physiol. A* 147: 195–200

92. Langer H, Haumann B, Meinecke CC. 1979. Tetrachromatic visual system in the moth *Spodoptera exempta* (Insecta: Noctuidae). *J. Comp. Physiol. A* 129:235–39
93. Langer H, Schmeinck G, Anton-Erxleben F. 1986. Identification and localization of visual pigments in the retina of the moth, *Antherea polyphemus* (Insecta, Saturniidae). *Cell Tissue Res.* 245:81–89
94. Laughlin SB. 1994. Matching coding, circuits, cells, and molecules to signals: general principles of retinal design in the fly's eye. In *Progress in Retinal and Eye Research*, 13:165–96. London: Pergamon
95. Lehrer M. 1998. Looking all around: honeybees use different cues in different eye regions. *J. Exp. Biol.* 201:3275–92
96. Lieke E. 1981. Graded and discrete receptor potentials in the compound eye of the Australian bulldog-ant (*Myrmecia gulosa*). *Biol. Cybern.* 40:151–56
97. Lin JT, Wu CY. 1992. A comparative study on the color vision of 4 coleopteran insects. *Bull. Inst. Zool. Acad. Sin.* 31:81–88
98. Lipetz LE, Cronin TW. 1988. Application of an invariant spectral form to the visual pigments of crustaceans—implications regarding the binding of the chromophore. *Vis. Res.* 28:1083–93
99. Lüdtke H. 1953. Retinomotorik und adaptationsvorgänge im auge des rückenschwimmers (*Notonecta glauca*, L.). *Z. Vergl. Physiol.* 35:129–52
100. Lythgoe JN. 1972. The adaptation of visual pigments to the photic environment. In *Handbook of Sensory Physiology*, Vol. 7, Part 1: *Photochemistry of Vision*, ed. H Dartnall, pp. 566–603. Berlin: Springer-Verlag
101. Matic T. 1983. Electrical inhibition in the retina of the butterfly *Papilio*. I. Four spectral types of photoreceptors. *J. Comp. Physiol.* 152:169–82
102. McCann GD, Arnett DW. 1972. Spectral and polarization sensitivity of the dipteran visual system. *J. Gen. Physiol.* 59:534– 58
103. McDonald CG, Hawryshyn CW. 1995. Intraspecific variation of spectral sensitivity in threespine stickleback (*Gasterosteus aculeatus*) from different photic regimes. *J. Comp. Physiol. A* 176:255–60
104. Meinertzhagen IA, Menzel R, Kahle G. 1983. The identification of spectral receptor types in the retina and lamina of the dragonfly *Sympetrum rubicundulum*. *J. Comp. Physiol.* 151:295–310
105. Menzel R. 1979. Spectral sensitivity and colour vision in invertebrates. In *Invertebrate Photoreceptors (Handbook of Sensory Physiology*, ed. H Autrum, 7(6A):503–80. Berlin: Springer-Verlag
106. Menzel R, Backhaus W. 1991. Colour vision in insects. In *The Perception of Colour*, ed. P Gouras, 6:262–93 London: Macmillan
107. Menzel R, Knaut R. 1973. Pigment movement during light and chromatic adaptation in the retinula cells of *Formica polyctena* (Hymenoptera, Formicidae). *J. Comp. Physiol.* 86:125–38
108. Menzel R, Shmida A. 1993. The ecology of flower colours and the natural colour vision of insect pollinators: the Israeli flora as a study case. *Biol. Rev.* 68:81–120
109. Menzel R, Ventura DF, Hertel H, de Souza JM, Greggers U. 1986. Spectral sensitivity of photoreceptors in insect compound eyes: comparison of species and methods. *J. Comp. Physiol. A* 158:165–77
110. Merbs SL, Nathans J. 1993. Role of hydroxyl-bearing amino acids in differentially tuning the absorption spectra of the human red and green cone pigments. *Photochem. Photobiol.* 58:706–10
111. Meyer-Rochow VB. 1980. Electrophysiologically determined spectral efficiencies of the compound eye and median

ocellus in the bumblebee *Bombus hortorum tarhakimalainen* (Hymenoptera, Insecta). *J. Comp. Physiol. A* 139:261–66
112. Michener CD, McGinley RJ, Danforth BN. 1994. The bee genera of North and Central America. Washington, DC: Smithson. Inst. Press. 209 pp.
113. Milliron HE. 1971. A monograph of the Western Hemisphere bumblebees (Hymenoptera: Apidae; Bombinae). I. The genera *Bombus* and *Megabombus* subgenus *Bombias*. In *Memoires of the Entomological Society of Canada*, ed. D Pielou, 80:1–80. Ottowa: Entomol. Soc. Can.
114. Minet J. 1994. The Bombcoidea: phylogeny and higher classification (Lepidoptera: Glossata). *Entomol. Scand.* 25: 63–88
115. Montell C, Jones K, Zuker C, Rubin G. 1987. A second opsin gene expressed in the ultraviolet-sensitive R7 photoreceptor cells of *Drosophila melanogaster*. *J. Neurosci.* 7:1558–66
116. Mote MI, Goldsmith TH. 1970. Spectral sensitivities of color receptors in the compound eye of the cockroach *Periplaneta*. *J. Exp. Zool.* 173:137–45
117. Mote MI, Wehner R. 1980. Functional characteristics of photoreceptors in the compound eye and ocellus of the desert ant, *Cataglyphis bicolor*. *J. Comp. Physiol.* 137:63–71
118. O'Carroll DC, Bidwell NJ, Laughlin SB, Warrant EJ. 1996. Insect motion detectors matched to visual ecology. *Nature* 382:63–66
119. Osorio D. 1986. Ultraviolet sensitivity and spectral opponency in the locust. *J. Exp. Biol.* 122:193–208
120. Osorio D, Averof M, Bacon JP. 1995. Arthropod evolution: great brains, beautiful bodies. *Trends Ecol. Evol.* 10:449–54
121. Osorio D, Bacon JP. 1994. A good eye for arthropod evolution. *BioEssays* 16:419–24
122. O'Tousa JE, Baehr W, Martin RL, Hirsh J, Pak WL, et al. 1985. The *Drosophila ninaE* gene encodes an opsin. *Cell* 40:839–50
123. Papatsenko D, Sheng GJ, Desplan C. 1997. A new rhodopsin in R8 photoreceptors of *Drosophila*—evidence for coordinate expression with Rh3 in R7 cells. *Development* 124:1665–73
124. Paul R, Steiner A, Gemperlein R. 1986. Spectral sensitivity of *Calliphora erythrocephala* and other insect species studied with Fourier interferometric stimulation (FIS). *J. Comp. Physiol. A* 158:669–80
125. Paulus HF. 1975. The compound eyes of apterygote insects. In *The Compound Eye and Vision in Insects*, ed. GA Horridge, pp. 3–19. Oxford, UK: Clarendon
126. Peitsch D, Feitz A, Hertel H, de Souza J, Ventura DF, Menzel R. 1992. The spectral input systems of hymenopteran insects and their receptor-based colour vision. *J. Comp. Physiol. A* 170:23–40
127. Pelzer A, Langer H. 1990. Das visuelle System des Eulenfalters *Spodoptera exempta* (Lepidotera, Noctuidae), eines tropischen Landwirtschaftsschädlings. *Naturwissenschaften* 77:457–64
128. Polaczyk PJ, Gasperini R, Gibson G. 1998. Naturally occurring genetic variation affects *Drosophila melanogaster* photoreceptor determination. *Dev. Genes Evol.* 207:462–70
129. Regier JC, Fang QQ, Mitter C, Peigler RS, Friedlander TP, Solis M. 1998. Evolution and phylogenetic utility of the *period* gene in Lepidoptera. *Mol. Biol. Evol.* 15:1172–82
130. Roig-Alsina A, Michener CD. 1993. Studies of the phylogeny and classification of long-tongued bees. *Univ. Kans. Sci. Bull.* 55:124–62
131. Rojas JC, Wyatt TD, Birch MC. 2000. Flight and oviposition behavior toward different host plant species by the cabbage moth, *Mamestra brassicae* (L.) (Lepidoptera: Noctuidae). *J. Insect Behav.* 13: 247–54

132. Roubik DW. 1989. *Ecology and Natural History of Tropical Bees*. New York: Cambridge Univ. Press. 514 pp.
133. Sacks O. 1997. *Island of the Color Blind*. New York: Knopf. 311 pp.
134. Sakmar TP. 1998. Rhodopsin: a prototypical G protein-coupled receptor. *Prog. Nucl. Acid Res. Mol. Biol.* 59:1–34
135. Salcedo E, Huber A, Henrich S, Chadwell LV, Chou W-H, et al. 1999. Blue- and green-absorbing visual pigments of *Drosophila*: ectopic expression and physiological characterization of the R8 photoreceptor cell-specific Rh5 and Rh6 rhodopsins. *J. Neurosci.* 19:10716–26
136. Schlecht P. 1979. Colour discrimination in dim light: an analysis of the photoreceptor arrangement in the moth *Deilephila*. *J. Comp. Physiol. A* 129:257–67
137. Schlecht P, Hamdorf K, Langer H. 1978. The arrangement of colour receptors in a fused rhabdom of an insect, a microspectrophotometric study on the moth *Deilephila*. *J. Comp. Physiol.* 123:239–43
138. Schmitz J, Moritz RFA. 1998. Molecular phylogeny of Vespidae (Hymenoptera) and the evolution of sociality in wasps. *Mol. Phylogenet. Evol.* 9:183–91
139. Schwemer J, Paulsen R. 1973. Three visual pigments in *Deilephila elpenor* (Lepidoptera, Sphingidae). *J. Comp. Physiol.* 86:215–29
140. Scott JA. 1986. *The Butterflies of North America: A Natural History and Field Guide*. Stanford, CA: Stanford Univ. Press. 582 pp.
141. Seki T, Vogt K. 1998. Evolutionary aspects of the diversity of visual pigment chromophores in the class Insecta. *Comp. Biochem. Physiol. B* 119:53–64
142. Shyue S-K, Hewett-Emmett D, Sperling HG, Hunt DM, Bowmaker JK, et al. 1995. Adaptive evolution in color vision genes in higher primates. *Science* 269:1265–67
143. Snyder AW, Menzel R, Laughlin SB. 1973. Structure and function of the fused rhabdom. *J. Comp. Physiol.* 87:99–135
144. Stavenga DG. 1992. Eye regionalization and spectral tuning of retinal pigments in insects. *Trends Neurosci.* 15:213–18
145. Stavenga DG, Smits RP, Hoenders BJ. 1993. Simple exponential functions describing the absorbancy bands of visual pigment spectra. *Vis. Res.* 33:1011–17
146. Steiner A, Rudiger P, Gemperlein R. 1987. Retinal receptor types in *Aglais urticae* and *Pieris brassicae* (Lepidoptera), revealed by analysis of the electroretinogram obtained with Fourier interferometric stimulation (FIS). *J. Comp. Physiol. A* 160:247–58
147. Struwe G. 1972. Spectral sensitivity of single photoreceptors in the compound eye of a tropical butterfly (*Heliconius numata*). *J. Comp. Physiol.* 79:197–209
148. Struwe G. 1972. Spectral sensitivity of the compound eye in butterflies (*Heliconius*). *J. Comp. Physiol.* 79:191–96
149. Sun H, Macke JP, Nathans J. 1997. Mechanisms of spectral tuning in the mouse green cone pigment. *Proc. Natl. Acad. Sci. USA* 94:8860–65
150. Sundin OH, Yan J-M, Li Y, Zhu D, Hurd JN, et al. 2000. Genetic basis of total colour blindness among the Pingelapese islanders. *Nat. Genet.* 25:289–93
151. Swihart SL. 1972. The neural basis of colour vision in the butterfly, *Heliconius erato*. *J. Insect Physiol.* 18:1015–25
152. Townson SM, Chang BSW, Salcedo E, Chadwell LV, Pierce NE, Britt SG. 1998. Honeybee blue- and ultraviolet-sensitive opsins: cloning, heterologous expression in *Drosophila*, and physiological characterization. *J. Neurosci.* 18:2412–22
153. Troje N. 1993. Spectral categories in the learning behaviour of blowflies. *Z. Natforsch.* 48c:96–104
154. Vishnevskaya TM, Shura-Bura TM. 1990. Spectral sensitivity of photoreceptors and spectral inputs to the neurons of

the first optic ganglion in the locust (*Locusta migratoria*). In *Sensory Systems and Communication in Arthropods*, pp. 106–11. Basel: Birkhäuser Verlag
155. Vogel S, Westerkamp C, Thiel B, Gessner K. 1984. Ornithophilie auf den canarischen inseln. *Plant Syst. Evol.* 146:225–48
156. Warrant E, Porombka T, Kirchner WH. 1996. Neural image enhancement allows honeybees to see at night. *Proc. R. Soc. London Ser. B* 263:1521–26
157. Weiss M. In press. Vision and learning in some neglected pollinators: beetles, flies, moths and butterflies. In *Cognitive Ecology of Pollination*, ed. L Chittka, JD Thomson. Cambridge, MA: Cambridge Univ. Press
158. Weller SJ, Pashley DP. 1995. In search of butterfly origins. *Mol. Phylogenet. Evol.* 4:235–46
159. Westrich P. 1989. *Die Wildbienen Baden-Württembergs*, Vols. I, II. Stuttgart, Germany: Ulmer Verlag. 972 pp.
160. White RH, Brown PK, Hurley AK, Bennett RR. 1983. Rhodopsins, retinula cell ultrastructure and receptor potentials in the developing pupal eye of the moth *Manduca sexta*. *J. Comp. Physiol.* 150:153–63
161. White RH, Stevenson RD, Bennett RR, Cutler DE, Haber WA. 1994. Wavelength discrimination and the role of ultraviolet vision in the feeding behavior of hawkmoths. *Biotropica* 26:427–35
162. Widmer A, Schmid-Hempel P, Estoup A, Scholl A. 1998. Population genetic structure and colonization history of *Bombus terrestris* s.I. (Hymenoptera: Apidae) from the Canary Islands and Madeira. *Heredity* 81:563–72
163. Williams PH. 1985. A preliminary cladistic investigation of relationships among the bumble bees (Hymenoptera, Apidae). *Syst. Entomol.* 10:239–55
164. Witt R. 1998. *Wespen*. Augsburg: Naturbuch Verlag. 360 pp.
165. Wittmann D, Radtke R, Cure J, Schifino-Wittmann MT. 1990. Coevolved reproductive strategies in the oligolectic bee *Callonychium petuniae* (Apoidea, Andrenidae) and three purple flowered *Petunia* species (Solanaceae) in southern Brazil. *Z. Zool. Syst. Evol.* 28:157–65
166. Yang E-C, Osorio D. 1991. Spectral sensitivities of photoreceptors and lamina monopolar cells in the dragonfly, *Hemicordulia tau*. *J. Comp. Physiol. A* 169:663–69
167. Yang I-F, Lin J-T, Wu C-Y. 1998. Fine structure of the compound eye of *Mallada basilis* (Neuroptera: Crysopidae). *Ann. Entomol. Soc. Am.* 91:113–21
168. Yokoyama R, Yokoyama S. 1990. Convergent evolution of the red- and green-like visual pigment genes in fish, *Astyanax fasciatus*, and human. *Proc. Natl. Acad. Sci. USA* 87:9315–18
169. Yokoyama S, Radlwimmer FB. 1999. The molecular genetics of red and green color vision in mammals. *Genetics* 153:919–32
170. Zufall F, Schmitt M, Menzel R. 1989. Spectral and polarized light sensitivity of photoreceptors in the compound eye of the cricket (*Gryllus bimaculatus*). *J. Comp. Physiol. A* 164:597–608
171. Zuker CS, Cowman AF, Rubin GM. 1985. Isolation and structure of a rhodopsin gene from *Drosophila melanogaster*. *Cell* 40:851–58
172. Zuker CS, Montell C, Jones K, Laverty T, Rubin GM. 1987. A rhodopsin gene expressed in photoreceptor cell R7 of the *Drosophila* eye: homologies with other signal-transducing molecules. *J. Neurosci.* 7:1550–57

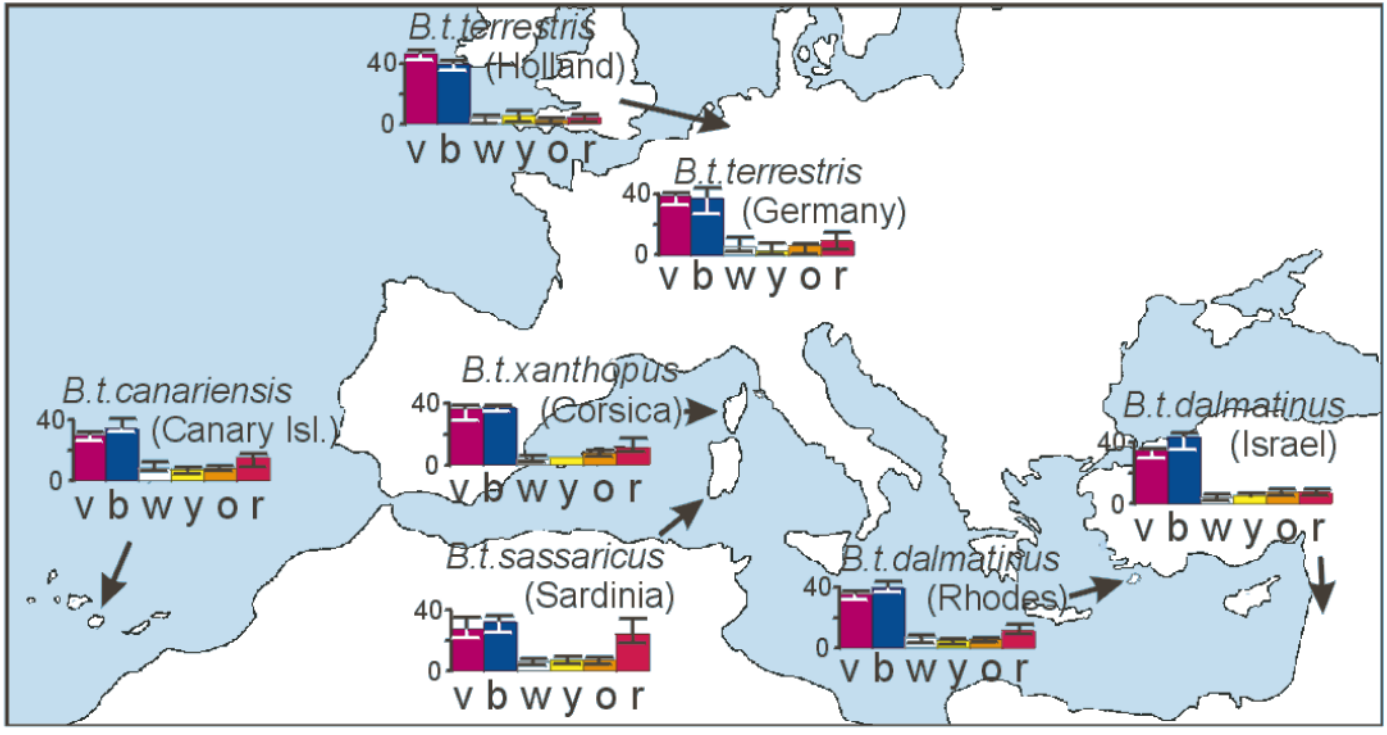

Figure 7 Biogeography of floral color preferences in *Bombus terrestris*. Bees were individually offered the colors violet (V; bee UV-blue), blue (B; bee blue), white (W; bee blue-green), yellow (Y), orange (O), and red (R) (the latter three are bee green). Column height denotes the percentage of cumulative choices of all bees from all colonies. Error bars show percentages for colonies with extreme values.

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